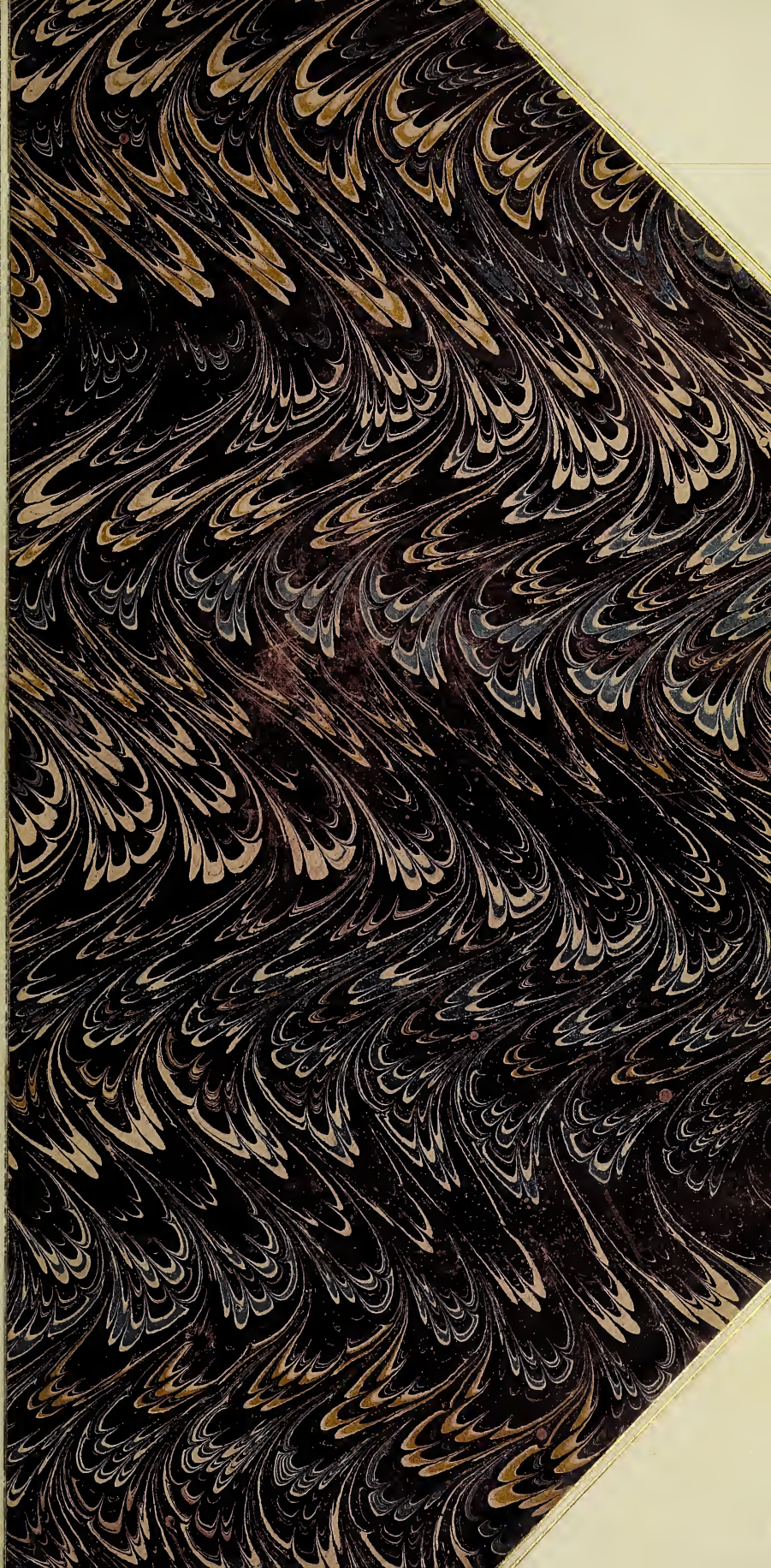

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ANNALS OF BOTANY

EDITED BY

ISAAC BAYLEY BALFOUR, M.A., M.D., F.R.S.
PROFESSOR OF BOTANY IN THE UNIVERSITY
AND KEEPER OF THE ROYAL BOTANIC GARDEN, EDINBURGH

SYDNEY HOWARD VINES, D.Sc., F.R.S.
FELLOW OF MAGDALEN COLLEGE, AND SHERARDIAN PROFESSOR OF BOTANY
IN THE UNIVERSITY OF OXFORD

AND

WILLIAM GILSON FARLOW, M.D.
PROFESSOR OF CRYPTOGAMIC BOTANY IN HARVARD UNIVERSITY, CAMBRIDGE, MASS., U.S.A.

ASSISTED BY OTHER BOTANISTS

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ERRATA.

P. 76, line 4, *for* derivation *read* derivatives.
P. 89, line 26, *for* petroleum, ether *read* petroleum-ether.
P. 113, line 31, *for* Harsten *read* Hartsen.
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P. 388, line 10, *for* Doulist *read* Douliot.
P. 428, line 22, *for* heliotropic *read* geotropic.

On the Life-history of Macrosporium parasiticum, Thüm.

BY

KINGO MIYABE.

With Plates I. and II.

MACROSPORIUM is found among a scanty list of the form-genera, whose affinity to certain Ascomycetes has been proved with different degrees of certainty. It is to the labours of Tulasne, Gibelli and Griffini, Bauke, and Kohl, that we owe to a great extent our present knowledge of its relation to the genus *Pleospora*, and also of the rest of the phases of its development, conflicting and unsettled in many important points as these may still be.

Early in the beginning of this year, a specimen of *Macrosporium parasiticum* on onion-plants from Bermuda was kindly placed in my hands for the study of its life-history by Prof. W. G. Farlow, under whose directions the present work has been done.

The Bermuda specimens which I have examined were so far advanced in decomposition that the course of the *mycelium* of the *Macrosporium* in its relation to the internal tissues of the leaves was not clearly definable. The mycelium, which was found in nearly every part of the leaves, sent out through stomata, and sometimes through the ruptured epidermis, small tufts of fertile hyphae. The number of the hyphae in each tuft varied with the size of the aperture, through which they protruded. In the case of the stomata, three to five seemed to be the common number (Fig. 1). These fertile hyphae were simple or occasionally branched, septate and smooth. Their length ranged from fifty to more than a hundred micro-

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millimeters. The average length, however, at which the first crop of the conidial spores was formed, was about seventy-five. The diameter of the hyphae at their central portion was five to six micromillimeters. They were generally somewhat swollen at their bases. The swelling was more constant and striking at their free ends, where the spores were borne (Fig. 1 *c*). These spore-bearing cells were always deeper brown in colour than the rest of the hyphae, and their walls were greatly thickened all around their lateral sides in the form of a band. But the wall of their terminal portions remained always thinner in texture and lighter in colour. It was often observed, therefore, that in some of the older hyphae which had ceased to grow after having shed their spores, their terminal walls collapsed and gave to the cells a characteristic cup-shaped form (Fig. 1 *e*). In those which were probably more favourably situated, and abundantly supplied with nourishment, a new growth of hyphae was seen to have taken place from the very spot where the spore had once been borne (Fig. 1 *d*). But a far more common form to be met with in the Bermuda specimens was one where a new growth took its origin, not from the swollen cell, but from the cell next below (Fig. 3). This new hypha grew right through the middle of the former, piercing the wall at its tip, and stopped in growth in most of the cases when two or three septa had been formed. At its free end a new spore was produced. This process could be seen to be repeated several times on a single hypha.

It was not uncommon to see a branch formed also on the upper part of the swollen cell. But in general the branches arose from any of the cells of the primary fertile hypha. The place of their formation on a cell appeared not to be constantly fixed. In some it was produced just below a septum, while in others at about a middle portion of the cell. The branch was usually short, and was given off at an obtuse angle; and on its end a spore was formed.

The spores varied greatly in form and size. In form, they ranged from oblong-obovate to depressed-rotundate, always rounded at both ends. They were furnished with three prin-

cipal transverse septa and a longitudinal one, usually with further subdivisions by oblique, transverse or longitudinal partitions, making them into five-, six-, or at times seven-septate muriform spores. Their wall was slightly constricted at the principal septa. It was covered to a greater or less extent all over the surface with very minute projections. This roughness of the spore was quite characteristic; though very rarely one might meet with a spore which looked perfectly smooth. The spore measured 33–43 by 18–23 m.mm., and the average size was about 37 by 21 m.mm. (Figs. 1 *f* and 2).

On the Bermuda specimens, besides the *Macrosporium*-spores, a large number of young perithecia were observed. Among numerous sections made on different portions of the leaves, I obtained only once the unripened resting-spores of *Peronospora Schleideniana*. The *Macrosporium*-spores were abundantly seen around the perithecia, with which it was proved that they have organic connection. The perithecia were still too young for the satisfactory determination of species. With regard to our *Macrosporium*, it has been clearly proved to be identical with *Macrosporium parasiticum*, Thümen, by careful comparison with authentic specimens. So far as I am aware, nothing has been published on the life-history of Thümen's species[1]. With a view to determine it as completely as possible, the following cultures were conducted.

The different culture-methods were followed according to the nature of the results to be attained. For observing the germination of the spores under the microscope, the formation of the perithecia, and the rest of the earlier stages of the development of the plant, the Van Tieghem cell was employed. For the study of its further development, the Erlenmeyer flasks proved to be most useful. For nutrient fluids, thin decoctions of onion, of date, of grape, and of horse-dung were used. The onion and date gave the most satisfactoryresults. Both fluids and apparatus had been carefully sterilised before any sowing was done.

Up to the end of March, fifteen cultures in the Van Tieghem

[1] [See Appendix to this paper. Ed.]

cells and twelve in the flasks were made. Except four failures with the former, the rest of the cultures were successful. Since that time, two more cell- and eight more flask-cultures have been prepared. But they were all poorer in growth, and produced few or no perithecia on the mycelium. By way of comparison, several open cultures on slides and watch-glasses were also prepared.

A large number of young onion-plants were started both from seeds and bulbs. The spores were sown on different parts of the leaves; and the pots were kept moist under bell-jars, with the exception of a few which were left uncovered. The greater part of the young seedlings were badly injured by nematoid worms; but those which survived did not show any sign of the attack. Out of the twelve bulbs, the culture on only two was successful. The spores, however, grew in both cases only on the sheath of the leaves, and not on the active green portions. One of them produced the *Macrosporium*-spores in small quantity, while the other formed in addition a large number of perithecia. These perithecia were arrested in growth when some of them were large enough to form paraphyses in their interior.

The spores sown in pure water germinated within eight hours. The germ-tubes were as a general rule produced from the cells situated on the convex portions of the spores. The number of the tubes from each spore varied a great deal according to its size. In a fully-grown spore, three to six tubes were most commonly seen. These tubes or hyphae grew rapidly in length, but produced lateral branches rather sparingly. The hyphae were colourless and septate, and were filled with refractive contents. The branches were slender and anastomosed readily with each other or with the main hyphae, when they happened to meet. As the hyphae grew in length, many of the cells lost the larger part of their contents, which were carried from one portion to another, until they settled in a certain part of the hyphae. Towards the end of the main hypha a very slender transparent branch was usually observed. The extremity of this branch regularly formed a closely coiled

spiral (Fig. 4). The portion of the hypha adjoining the spore increased in diameter, forming a row of roundish cells for a short distance.

Besides these colourless vegetative hyphae, which grew in the fluid, some of the spores produced directly on their surface short stout filaments of a brownish colour which grew into the air. In cell-cultures, four days after the sowing, secondary spores were observed on their ends. They were then still small, ovate or oblong in form, and one to three septate; and their wall was smooth and light brown in colour. In some way or other their further growth was arrested. The spore-bearing hyphae corresponded very closely in their characters and proportion to those of the Bermuda specimens already described.

In open cultures with pure water the secondary spores were also produced abundantly. On the fifth day they were found to have grown to about one-half the size of mother-spores, and they continued to grow until they were ripe. They showed all the characteristics of the *Macrosporium*-spores. Only in a few cases have I been able to see the spore-bearing filaments produced on the hyphae proceeding from the spores sown. There were no signs of the formation of perithecia in any of the water-cultures.

On the other hand, the spores which were sown in a nutrient fluid presented a widely different result. The main hyphae coming directly out of the spores were vigorous and grew radially at the rate of about 0.6 mm. daily for the first day or two, the rate of growth increasing at quite a rapid ratio until about the fifth day of the culture, when it gradually decreased. On the third day, the average growth during twenty-four hours was 1.8 mm.; on the fifth day, 2.5 mm.; and on the sixth day, about 1.5 mm. They gave out lateral branches in large number, which, interlacing and anastomosing with each other, formed at the end of two days a mycelium of about 3 mm. in diameter. The main hyphae were easily distinguished by their larger size and straighter course, and also by their being copiously filled with fatty globules and

glycogen, as ascertained by the iodine test. Their wall soon assumed a light yellowish brown colour.

On these main hyphae, and very rarely on their larger branches, some of the earliest perithecia were formed during the second and third days of the culture. The first sign of their formation was the division of a certain portion of the hypha into a row of short cells. One or usually two or more of these cells began to swell considerably, and each of them sent out one or more hyphal branches, before any division took place in them (Fig. 7). The branches were at first very slender and hyaline; and they grew very rapidly, anastomosing with remarkable readiness with each other, and with any other hypha which happened to lie in their course.

While the branches were thus growing, the initial cell or cells continued to swell and divide, first into two by a transverse or oblique septum, and then into four or more, and so on. There seemed indeed to be no regular directions in the cell-divisions. The resulting tissue was parenchymatous in structure, and the cells composing it were so closely united as to leave scarcely any intercellular space between them. The basal portions of the hyphal branches mentioned above began at the same time to swell and divide (Fig. 8). The groups of cells thus formed, coalescing with the central tissues, gave to perithecia at this stage most irregular forms with several projections (Fig. 9). But as they went on growing and dividing, they sent out from the newly formed outside cells an additional number of similar branches. Their basal parts again by growth and division contributed new groups of cells to the growing central mass; and thus the young perithecia gradually assumed a definite globular shape. At the beginning of the culture, all the changes and growth took place within twenty-four hours in a vigorously growing plant; while in those perithecia formed later on, when the nourishment had become somewhat scarce, it took about three or more days for a similar amount of growth.

On the fourth or fifth day after the sowing, the outside layer of cells of a young perithecium began to assume a dark

colour. The colour was at first deeper on those portions most exposed to light. They were then easily recognisable with the naked eye as small black spots on the mycelium.

While the perithecia were thus being formed, many other important changes were also taking place on the growing mycelium. Besides the growth of the mycelium along the surface of the fluid, a large number of hyphae were sent out both upwards into the air, and downwards into the liquid substratum. Those that were sent down into the fluid were finer than those on which the perithecia were formed. They remained colourless for a long time. In some cases they presented a peculiar undulating appearance, which reminded one of the rhizoids of a *Marchantia*. Generally they formed a loose fringe of a light colour, hanging down into the fluid. But in some of the flask-cultures, where an excessive growth of hyphae took place, they formed a thickly interlaced felt of dark brown colour, with many young perithecia entirely immersed at first in its tissue just under its upper surface.

The aerial hyphae were generally observed two days after the sowing on the central or older part of the mycelium, as short white filaments. They were at first more or less erect, but as they grew on, they began to trail, forming a cobwebby veil over the surface. On these hyphae were produced short branches, which were given out perpendicularly, and which bore on their tips the *Macrosporium*-spores. These fertile hyphae were also formed on the mycelium as well as on some of the perithecia. The aërial hyphae began to assume a light brownish colour at about the time when the spores were forming.

The earlier *Macrosporium*-spores were observed on the third day of a culture. On the fifth day they were ripe, and even produced on their surface the secondary spores having all the characteristics of the spores themselves.

The fertile hyphae were similar in size and characters to those of the Bermuda specimens, with a few minor variations caused by the difference in substrata. They were produced in the present case, not in tufts, but scattered singly on the

hyphae; and there were no swellings to be seen at their bases.

The spores were formed as a general rule from the terminal portions of the fertile hyphae by abstriction. The cell, from which both the spore and swollen spore-bearing cell (basidium) were to be formed, was at first tapering towards its free end (Fig. 5 *a*). The abstriction took place usually at a point a little above its middle part, without being at the same time accompanied by the formation of a partition. The lower half attained its full size while the spore-portion was yet small. The latter was at first ovate in form, colourless, and smooth (Fig. 5 *c*). The roughening and darkening of its cell-wall began to take place when two or three cross-partitions were formed in the spore. In the course of a few days the spore ripened and presented its characteristic muriform shape. The connection between the spore and basidium was very slight. As a consequence, the ripened spore fell off at the least disturbance.

In closed cultures, however, where the plants were kept undisturbed, the ripened spores remained on the hyphae for a long time. It was very rare to see the new spores produced at the ends of the newly extended hyphae proceeding from the tips of the old ones, as commonly observed in the Bermuda specimens. Instead of this process, the new crops of spores were produced here mostly as secondary spores on the surface of the ripened spores. They were produced at the ends of short hyphal branches, which were given out perpendicularly from different parts of the spores. Some of the spores produced three, four, or even more secondary spores on their surface at the same time. On these secondary spores another crop of similar spores was rarely observed while the whole arrangement was still borne on the tip of the hypha.

Another mode of spore-formation, which was far less common than that described above, was one where a new spore was produced on the tip of a fertile hypha by the side of an old spore, which was shifted a little to one side. Here the abstriction of the sprouting hypha took place very close to the surface of the swollen basidium, resembling somewhat the

budding of a yeast-plant. The spore, when it was ripe, could not be distinguished from the older one by its side (Fig. 6).

This 'budding' process may be more common than I am aware in the spore-formation of this plant. I have observed several instances which strongly suggested this process; but, as I did not observe their earliest stages, I cannot state here positively its occurrence beyond the case just described.

Concerning the further development of the perithecia, it will be convenient to take a plant about a week old and follow its development. The mycelium was then blackish in colour, and full of young perithecia and *Macrosporium*-spores in different stages. The oldest perithecia were about 0.2 mm. in diameter. They were generally globular in shape. Their internal structure was still undifferentiated, being composed of cells of similar shape and size, and equally filled with glycogen and fatty matters.

The growth and division of the cells continued to take place in all parts of the perithecium. The cells towards the outside began to grow more rapidly in size than those in the central part, where the cells remained almost at their original size, as they multiplied by constant growth and division. A large number of the cells in the central portion then became markedly filled with very refractive contents. Their number and position in the perithecium were variable, and could not be stated definitely. As to the position, sometimes they were found in the upper portion, sometimes in the lower, but commonly near the centre of the perithecium. These cells soon began to elongate and divide mostly in an upward direction, forming a body of short irregular chains of cells, which might be either simple or branching (Figs. 10 *d* and 11 *b*). From the tip of each of these chains of cells, one, two, or rarely three slender hyphal branches were sent out (Fig. 11, *B*, *C*). The branches or *paraphyses* thus formed in large number, at first crossed each other to a greater or less extent. They, however, soon took a definite upward course in a closely packed bundle towards air and light. The larger part of the parenchymatous cells lying above in the way of these rapidly-

growing paraphyses seemed to be dissolved away, their places being occupied at once by the latter.

This internal change was accompanied by the general growth of the perithecium. The growth was especially active in the upper portion, which was prolonged into a short blunt beak. The bundle of paraphyses grew into the beak, forming a comparatively broad canal, and ceased to grow when it reached the external layer of the obtuse tip, on which usually more than one short papilla was found.

The paraphyses were filiform, septate, and simple, or very rarely branched. They were then copiously filled with glycogen and fatty matters. The perithecia ceased to grow in size when the paraphyses in their interior had reached their full development. All subsequent changes in the interior attending the growth of asci produced little or no effect on the external configuration of the perithecium.

About two weeks after the sowing, a large number of asci began to grow among the rows of paraphyses. The asci were formed as branches on some of those cells from which the paraphyses had sprung (Figs. 10 *e* and 12 *A*). They were at first somewhat club-shaped, and were full of colourless granular protoplasm free from glycogen. The growth of the asci generally began to take place when the bundle of paraphyses had reached its full size. I have observed a few cases, however, in which the asci had grown to about the length of the paraphyses, when the latter were still at about two-thirds of their growth.

In an ascus which had attained the length of about 70m.mm., that is about one-half its full size, a globular nucleus was observed in its upper portion (Fig. 13 *A*). In one which had progressed a little further, eight spore-primordia made their appearance. When they were surrounded by a cell-wall, they were first divided into two by a transverse septum at the middle, then into four by two septa parallel to the first one (Fig. 12 *B*). At this stage, the spores were colourless and spindle-shaped; and the ascus was still copiously filled with granular colourless protoplasm. Before any further division

in the spores took place, they began to grow noticeably in width, and to assume a yellowish colour (Fig. 12 *C*). At about this stage, in some of the spores, a longitudinal partition was formed for the first time.

It took just about a month from the beginning of the formation of a perithecium to the full ripening of its ascospores. A large number of the asci, which were often very closely packed in the cavity of the perithecium, exerted a considerable pressure on the parenchymatous cells along its side, causing them to flatten, and also on the paraphyses between them. The paraphyses lost a considerable part of their contents. Their outline became indistinct, and in some places their cell-wall became completely mucilaginous. The same changes took place in the basal cells, from which both paraphyses and asci were formed. The refractive contents, which had once filled these cells, must have been used up in the formation and growth of the asci and ascospores.

The matured asci were cylindrical-oblong in shape, tapering at one end into short curved pedicels, which were slightly dilated at the point of attachment. Their size ranged from 120 to 160 m.mm. in length, and from 25 to 30 m.mm. in width. The spores were arranged mostly in two ranks, but towards the base of the ascus they were frequently one-ranked. The spores, even the well-matured, were enveloped in a thin layer of protoplasm, which united the whole into a group. The spores were elliptical or oblong, obtuse at both ends, and 7-septate, with two or three longitudinal partitions at the middle portion, and one or two towards both ends. They were constricted at about the middle. The upper portions were always larger than the lower. They were yellowish-brown in colour, and in size from 30 to 33 m.mm. in length, and 12 to 15 m.mm. in width (Fig. 13).

In typical cases, the fully matured perithecia were slightly depressed globular in form, with short obtusely-conical beaks, and with flattened bases. Those perithecia which were formed crowded together on a mycelium had longer and narrower forms, with prominent beaks. It was not rare to

see two or more perithecia completely coalesced into one irregular body. The size of the perithecia varied a great deal; but commonly it was between 300 and 450 micromillimeters in diameter.

When a ripened ascus was placed free in water, it began in a few minutes to elongate a little with a corresponding slight diminution in diameter. The internal tension continually increasing by the rapid absorption of water caused finally the rupture of the outer layer of the wall, possessed of a limited power of extensibility, at the apex of the ascus. Relieved of the external resistance, the inner layer elongated in a short time (5–10 seconds) to about two and a-half times the original length of the ascus, carrying with it the spores and protoplasmic envelopes. In none of a large number of the free asci observed under water was there any ejection of the spores from the tips of the elongated tubes. Every one of them germinated in the asci just as they were grouped, sending the hyphae through the delicate wall of the tubes.

Two matured perithecia were placed in a moist chamber, and kept overnight. The next morning it was found that a large number of the spores had been ejected, some to the distance of seven millimeters. But the greater part of the spores dropped near the ostioles. They were scattered, and not in groups of eight. During the night, every one of them had germinated. It is quite probable that the spores in the present case might have been ejected successively from the tips of the elongated asci, which forced their way through the very narrow orifices of the papillae, after the manner of some of the allied plants, as *Sphaeria Lemaneae*.

The ascospores when sown in nutrient fluids germinated of and grew vigorously, just in the same manner as in the case the *Macrosporium*-spores. In every sowing of the ascospores, only the perithecia and *Macrosporium*-spores were formed on their hyphae. Pycnidia and other forms of conidia, generally attributed to *Pleospora*, have not been observed in any of my closed cultures.

Before determining the specific position of our plant, it may

not be out of place here to state concisely the results of my examination of Thümen's original specimens of *Macrosporium parasiticum*[1]. They are not so much advanced in growth as the Bermuda specimens; still the spores are well matured. Their size and shape correspond very closely with those of the latter. They have also the characteristic minute projections over their surface, though this characteristic is not mentioned in his description. The number of tranverse septa is usually five to seven. I have not been able to find a spore which has so many as ten septa. The fertile hyphae correspond exactly in all essential characters in both specimens (Fig. 16). It is beyond doubt that the Bermuda *Macrosporium* is identical with the European form described by Thümen.

From the preceding account of the development of the *Macrosporium parasiticum* it will be clearly seen that its ascosporic stage is a species of *Pleospora;* and furthermore, that it corresponds so closely in every essential character to the descriptions and figures of *Pleospora herbarum* (Pers.), Rabenh., given by Berlese[2] in his recent monograph, and also to those by Tulasne[3], von Niessl[4], and Winter[5], as to leave little doubt in regard to their identity. The comparison with the authentic specimens of *Pleospora herbarum* in the European exsiccati further confirmed the point in question[6].

[1] F. de Thümen, Mycotheca Universalis, Cent. vii. n. 667, Klosterneuburg, 1887. Accompanied by the following description:—'Maculas atras formans; hyphis abbreviatis breviarticulatis, ramosis, ramis brevibus, griseo-fuscis; conidiis oblongo-ovoideis vel ovoideo-rotundatis vel clavatis, 6–10 septatis, utrinque obtusis, 42–48 × 10–16, fuscis. Hab. in foliis vivis vel languidis *Allii Cepae*, praecique in *Peronospora Schleideniana* parasitans. Bayreuth Bavariae.'

[2] A. N. Berlese, Monografia dei generi *Pleospora*, *Clathrospora* e *Pyrenophora*, in Nuovo Giornale Bot. Ital. vol. xx. 1888, No. 1, p. 91, tav. v. f. 2–6.

[3] L. R. et C. Tulasne, Selecta Fungorum Carpologia, tom. ii. 1863, p. 261, tab. xxxii–xxxiii, Fig. 10–14.

[4] G. von Niessl, Notizen ueb. neue u. krit. Pyrenomyceten, p. 29, tab. iv, Fig. 14, 1876.

[5] G. Winter, Rabenh. Kryptog. Flora, Bnd. I. 1885. Pilze, ii. p. 504, Fig. on p. 408.

[6] Some of the specimens on the onion-plants were carefully examined and compared. One published by Cesati and de Notaris under the name of *Pleospora Allii* in Herb. Critt. Ital. ser. ii. fasc. xiii. n. 644, was mostly too young. I saw one or two asci, whose spores were somewhat advanced towards maturity. In some of

The forms of *Pleospora herbarum* growing on onions were once considered by Rabenhorst, Saccardo, and many other authors as a distinct species from, or a variety of, that common fungus. They are, however, at present included under that species without any restriction by the authors who have studied the genus critically, as Berlese, Winter, von Niessl, and some others. The examination of some of the authentic specimens, and also observations on the development of the plant, induce me strongly to accept the latter view.

It has been well established that *Macrosporium Sarcinula* of Berkeley has a genetic connection with *Pleospora herbarum*. Is then *Macrosporium parasiticum*, Thüm., identical with *M. Sarcinula*, or is it another form of the conidial stages of this remarkable plant? Unfortunately, I have not been able to examine the original specimens of Berkeley's species. From his descriptions and figures[1] of the plant, I found it rather hard to make a very satisfactory comparison with our plant. But according to the descriptions and figures of the same plant by Tulasne[2], there exists such a striking resemblance between these two species of *Macrosporium*, that any one unprejudiced would at once accept them as of one and the same species. Their identity is further confirmed by the fact, that both can produce on their mycelium perithecia which could not be distinguished one from the other.

The only apparent difference that still remains between the *Sarcinula* and *Macrosporium*-forms is their habitat. The former has generally been considered to be entirely saprophytic; while it has been proved that the latter not only thrives on dead vegetable matters, but can also grow on the living plant

these spores the partitions were not fully formed. Still, they were sufficiently grown to exhibit the characteristics of the species (Fig. 15).

Sphaeria herbarum, Pers., on *Allium Cepa* in Wartmann and Schenk, Schweiz. Krypt. n. 322, was in a far better condition. It coincides in every respect with my plant (Fig. 14).

[1] M. J. Berkeley, Notices of British Fungi, Ann. Nat. Hist. vol. i. No. 4, 1838, p. 261; No. 125, Pl. viii. f. 10.

[2] Tulasne, l.c., p. 263, tab. xxxii. Fig. 6.

accompanying a stronger parasite, as *Peronospora Schleideniana*, or by attacking a plant on its less active tissue, as the sheath of the onion-plant. A statement was however made by De Bary [1] on the possibility of species of *Pleospora* being classed among facultative parasites. In fact, observations in regard to the parasitic nature of *Pleospora herbarum* are not wanting. Spegazzini [2] has found this fungus on the living leaves of grape-vine and *Medicago sativa*; Cugini [3] and Passerini [4] on living branches of mulberry-trees; Berlese [5], on branches of *Sambucus nigra*; and Linde [6], on roots of clover. These observations however few in number, supported by our own cases on onion-plants, give us sufficient ground to consider *Pleospora herbarum* as a facultative parasite.

It is now convenient to briefly state some of the main points we have arrived at so far. It has been proved that the ascosporous stage of *Macrosporium parasiticum* of Thümen is the common *Pleospora herbarum*, and that the so-called *M. parasiticum* itself is nothing more than *M. Sarcinula* of Berkeley growing on onion-plants.

One seldom meets with a plant whose life-history has been beset with so much confusion, and about which so many controversies have been left unsettled for a long time, as *Pleospora herbarum*, the plant we have just been considering. The first important work on the subject was by Tulasne in 1863 [7]. He found in this plant a remarkable illustration of his theory of pleomorphism. He included under the name of *Pleospora herbarum* a perithecial, a pycnidial, and four conidial forms. Among the latter he distinguished, 1st, the *conidia dematiea*,

[1] De Bary, Vergl. Morphol. u. Biol. d. Pilze, p. 409, Leipzig, 1884; Eng. trans. p. 380.

[2] C. Spegazzini, Ampelomiceti italici: Funghi parassiti al grappolo, p. 726, 1878.

[3] G. Cugini, Intorno ad alcune malattie comparse nel 1884 su varie piante coltivate, in L'Agricoltura italiana; an x. Firenze, 1884, Nos. 120, 121.

[4] G. Passerini, Ancora della nebbia o nuova malattia dei gelsi e di alcuni altri alberi, in Bolletino d. Comizio agrar. parmense, Parma, 1884.

[5] Berlese, l. c. p. 99.

[6] S. Linde, Ueber Kleemüdigkeit des Bodens. Leipzig, 1880.

[7] Tulasne, l. c.

which correspond to *Cladosporium herbarum*, Lk.; 2nd, the *conidia didyma*; 3rd, those which correspond to *Macrosporium Sarcinula*, Berk.; and 4th, the *Exosporium conidia* (*Alternaria tenuis*, Nees.)

Fuckel[1], in 1869, added to the forms of Tulasne *Epicoccum herbarum* as one of the macroconidia of the plant. About the same time Hallier[2] claimed to have proved, by cultivations, that to *Pleospora herbarum* belong not only the six forms of Tulasne, but also a large number of others, namely, *Penicillium grande*, *Rhizopus nigricans*, *Oidium lactis*, an *Aspergillus*, a *Mucor*, *Stachylidium*, *Fumago*, *Micrococcus*, etc.

In 1873 Gibelli and Griffini[3] undertook to prove by means of a large number of careful cultures, in closed chambers, the assertions of the preceding authors. They came to the conclusions that *Pleospora herbarum* of Tulasne is to be divided into two distinct species, one constantly producing the *Sarcinula*-conidia (in which they included the second and third conidial forms of Tulasne) and the larger ascospores named by them *Pleospora Sarcinulae*; and the other, always the *Alternaria*-conidia, accompanied by the perithecia having smaller and less-septate ascospores, called *Pleospora Alternariae*. They obtained pycnidia only twice in the cultures of the ascospores which produced the *Sarcinula*-conidia. The pycnidia thus obtained were shown to be distinct from *Phoma herbarum*; and their pycnospores when sown constantly reproduced the pycnidia and nothing else. *Cladosporium herbarum*, *Epicoccum*, and Hallier's forms, they proved to have no genetic relations at all with either of their species of *Pleospora*.

They made also some observations on the development of

[1] L. Fuckel, Symbolae mycologicae, p. 130, 1869.

[2] C. Hallier, Untersuchungen des pflanz. Organismus, welcher die, unter d. namen *Gattine* bekannte Krankheit der Leidenraupen erzeugt. Potsdam, 1868. Die Muscardine des Kieferspinners, in Zeitschrift für die Parasitenkunde, Bnd. i. p. 18.

[3] G. Gibelli e L. Griffini, Sul polimorfismo della *Pleospora herbarum*, Tul., in Archivio Triennale del laboratorio di botanica crittogamica in Pavia, vol. i. pp. 53–102, tav. v–ix. 1874.

the perithecia of *Pleospora Sarcinulae*[1]. These arose, according to the authors, from two cells or sometimes from a single cell of the moniliform hyphae. The cells swelled up and divided, division taking place in various ways, so that they finally formed spherical cellular bodies. In one case a short lateral hypha incurved over the two initial cells was observed, which also played a part in their further development[2]. They were in doubt whether there was really anything like a fecundation of oogonia by the action of a pollinodium in this case.

In 1876, while Bauke[3] was engaged in the study of pycnidia of Sphaeriaceae, he met a doubtful case in *Pleospora herbarum*, which caused him to make a very large number of cultures. Thus he was led to study the other phases of its life-history at the same time. The preliminary communication[4] of the results he obtained was published in the year following. It is to be regretted that he left the work unfinished.

The conclusions he had arrived at were much nearer to Tulasne's than to Gibelli and Griffini's in regard to the question of pleomorphism. He included under *Pleospora herbarum*, besides an ascosporic stage, a pycnidial, *Sarcinula-*, *Alternaria-*, and microconidial forms. The last form, according to him, has hitherto been overlooked in consequence of the minuteness of its size.

He had some doubts about his pycnidia. He obtained them only twice in a very large number of the sowings of the ascospores. Though he failed to observe the direct organic connection between the latter and the pycnidia, he was convinced of the possibility of their connection by their peculiar forms, which at once distinguished them from all other pycnidia he knew of, and further by the fact that, by sowing the pycnospores, he obtained, besides the similar

[1] l. c. p. 82.

[2] l. c. tav. vii. Figs. 8-10.

[3] H. Bauke, Beiträge zur Kenntniss der Pycniden, i, in Nova Acta, Bnd. xxxviii. No. 5, p. 443. Taf. 28–33. Dresden, 1876.

[4] H. Bauke, Zur Entwickelungsgeschichte der Ascomyceten. Vorläufige Mittheilung, in Bot. Ztng. 1877, p. 313.

pycnidia, the characteristic *Alternaria*-spores. He never observed the pycnidia accompanied by the perithecia or *Sarcinula*-spores in the same culture.

He further states, that in the cultures of the ascospores obtained from perithecia growing on the same individual host-plant, or even from one and the same perithecium, some produced always the *Sarcinula*-spores and perithecia; while the others, always the *Alternaria*-spores alone, or, in two cases only, with the pycnidia also. The microconidial form finally appeared regularly on both sorts of the cultures. Bauke draws the conclusion from these facts, that mycelia of two different characters belong to this same species. With him the *Alternaria*-spores, when sown constantly, reproduced the *Alternaria* alone; and the *Sarcinula*-spores, regularly the perithecia and the *Sarcinula*.

His account of the formation and development of the perithecia coincides nearly with that given by Gibelli and Griffini. He refuses to consider those hyphae which sometimes happen to fasten on to the primordia of the perithecia as pollinodia. According to him, the formation of the perithecia is entirely apogamic.

He describes further the inner changes of the growing perithecia, which were scarcely touched upon by the Italian authors. In from three to five weeks the formation of paraphyses began to take place. From a number of parenchymatous cells, situated generally near the base of the perithecia in nearly the same plane, a bundle of thickly crowded hyphae or paraphyses sprang out upwards. The tissue situated in the place, which was eventually to be occupied by the growing paraphyses, was gelatinised and absorbed.

The perithecia formed in early spring produced the asci in the same season; but those formed later on in summer usually refused to grow after the formation of paraphyses had begun. In this state they passed the winter as sclerotia. The asci were formed as the branches of the basal cells of paraphyses. The contents of the latter contributed the nourishment for the growth and ripening of the ascospores.

Besides these, he observed regularly on the *Alternaria*-mycelium resting-hyphae of a very simple nature. Sometimes there appeared later in cultures peculiar hyphal bodies, which were dichotomously branched and parallel to one another. These bodies he considered as diseased formations caused by the nutrient fluids.

In 1882 Kohl[1] started a large number of cultures to settle the disputed problem of pleomorphism of the plant in question. Briefly, he came to the following conclusions: (1) that in pure cultures he obtained, by sowing the ascospores, only the *Sarcinula*-spores and the perithecia, and by sowing those *Sarcinula*-spores he obtained constantly a similar result; (2) that the *Alternaria*-spores when sown always produced the *Alternaria*-spores only; (3) that on the mycelium from the pycnospores the pycnidia and *Alternaria*-spores were formed; and (4) that *Cladosporium herbarum*, Bauke's *Microconidium*, and *Epicoccum* could not be found in the development-cycle of *Pleospora herbarum*.

He adopts the view of the Italian authors in separating the *Sarcinula*- and *Alternaria*-forms into two distinct species.

Berlese, in his recent monograph of the genus *Pleospora* already referred to, places *Pleospora Sarcinulae* of Gibelli and Griffini under *P. herbarum*, and their *P. Alternariae* under *P. infectoria*, Fuckel. They are the two most common species of the genus, and grow on about the same host-plants.

First, in regard to the question of the pleomorphism, the results of my cultures correspond exactly with those of Kohl. As has already been stated, the *Macrosporium*- or *Sarcinula*-spores, when sown in a nutrient fluid, constantly produced the perithecia and the *Sarcinula*-spores; and the ascospores from the perithecia thus obtained always reproduced similar perithecia and *Sarcinula*-spores. I have also failed to obtain pycnidia in any of my cultures of the ascospores.

The accounts of the pycnidia given by Gibelli and Griffini, and also by Bauke, are far from being convincing. The

[1] F. G. Kohl, Ueber den Polymorphismus von *Pleospora herbarum*, Tul., in Bot. Centr., Bd. xviii. 1883, p. 23.

uncertainty of their appearance, and the lack of definite observations in both cases on the direct organic connection between the ascospores sown and the pycnidia obtained, and also the constant failure in the attempt to reproduce the perithecia and *Sarcinula*-spore by sowing the pycnospores, lead one naturally to suspect that perhaps some foreign pycnospores may have been introduced into their cultures. Moreover, according to Kohl[1], the pycnospores enveloped in gelatinous substance, after oozing out in a vermiform mass, fasten more or less readily to a substratum, and send out into the air short slender hyphae, which terminate with small secondary spores (Luftsporen). They are very readily blown away by wind, or even by a slight breeze. They germinate on a wet substratum with great readiness.

The evidences of our investigations thus far lead us to the conclusions, that the presence of the pycnidia in *Pleospora herbarum* is very doubtful, and that they may have disappeared altogether from its cycle of development.

During the course of the present experiment an *Alternaria*-form repeatedly appeared on the label-papers pasted on the slides with Van Tieghem cells, which were kept moist under a bell-glass. It was often accompanied by *Penicillium* and *Hormodendron*. The same kind of *Alternaria* made its appearance about a year ago in the same laboratory on the decaying juniper-twigs kept for another purpose under a bell-glass. Its size, form, and habit correspond exactly with those of *Alternaria tenuis*, Nees, a form generally associated with *Pleospora herbarum*.

This *Alternaria*-spore was sown in different nutrient fluids. In flask-cultures it produced a mycelium, which grew with great rapidity, forming a thick and close mycelium. On its upper surface a very large number of aerial hyphae were produced, which were white at first, but gradually turned from green to grey, as the spores were formed and matured on them. The whole surface was literally packed with the rank

[1] Kohl, l. c. p. 30.

growth of long and branching chains of the *Alternaria*-spores, and no other forms of reproductive organs were to be found.

In Van Tieghem cells, the mycelium behaved differently from that of the *Sarcinula*-spore. The hyphae were straighter, and slightly smaller in diameter, and they turned quickly to a brownish colour. *Alternaria*-spores were abundantly formed. No signs of the formation of a perithecium or pycnidium were observed during the whole cultures, except in one instance on the mycelium of a half-starved old culture, when a process which might be taken as an attempt at the formation of either pycnidium or perithecium appeared.

I agree with Gibelli and Griffini and with Kohl in discarding *Alternaria tenuis* as a stage of *Pleospora herbarum*.

In regard to the formation and development of the perithecia, my observations coincide in the main with those of Bauke described in his preliminary communication. Like him I have been unable to observe any sexual process connected with the formation of the perithecia, nor have I been successful in finding any trace of the Woronin's hypha in a young perithecium before the formation of paraphyses and asci. The formation of the perithecium is entirely a vegetative process, which resembles essentially the formation of pycnidia. I do not consider the initial cells of the perithecia as degenerated female organs or ascogonia, but as entirely of vegetative origin.

Both in the *Alternaria*- and *Sarcinula*-cultures I have observed the resting-hyphae, which were briefly described by Bauke. In the *Sarcinula*-cultures started in May these bodies were commonly formed on the mycelium floating free on the surface of the culture-fluid. Besides these common forms of the resting hyphae, I observed in the earlier part of the experiment varieties of abnormal hyphae in the Van Tieghem cell-cultures of the spores of *Pleospora herbarum*. As the growth and appearance of these bodies are very remarkable and interesting, I may give a brief description of them before closing this paper.

In the *Sarcinula*-cultures, about five days after the sowing, a large number of club-shaped branches, filled with hyaline

highly refractive contents, made their appearance mostly towards the outer edge of the mycelium. These branches were produced close to the under-surface of the cover-glass, from which a drop of the culture-fluid was hanging. Fig. 17 represents one of the typical forms. Two cells at the extremities were still hyaline. Each of them sent out a branch, the lower one touching the upper. Two days after, it presented an unexpected appearance, as shown in Fig. 18. The upper of the two hyaline cells grew and divided, and produced a stout branch almost at a right angle. This branch produced again another branch at about a similar angle. As to the two branches mentioned in the first stage, the upper one did not grow, while the lower grew straight on and anastomosed with another hypha. The cells were soon filled with fatty globules, and ceased to grow. The cell-wall began to assume a brownish colour after some days. The whole arrangement remained unchanged until the end of the culture.

At another part of the same culture a similar process (Fig. 19) was watched. Here apparently two branches from the adjoining cells formed close spirals; and already several branches were formed upon them. During the next twenty-four hours a great change took place. A stout branch made a remarkable growth, and produced (at Fig. 20 *b*) a fast-growing branch, and (at *c*) a spiral process, which is represented highly magnified in Fig. 21. Two days after, two strong branches were found proceeding from the spiral process (Fig. 22). As in the first case, the cells became filled with fatty globules and stopped their growth. Fig. 23 represents one of the simpler forms of these peculiar bodies.

On the hyphae of the ascospores, these abnormal processes were produced more abundantly. But the spiral process was not observed. Here most of the branches swelled at their basal portions and divided into a row of a few large rounded cells. From the tip of the branches, a hyaline slender hypha, which was commonly slightly club-shaped at the end, was produced. The process at this stage resembled most remarkably a trichogyne and archicarp of some simple Floridean.

Usually, in a day or two, some branches were sent out from the rounded cells at the base. These branches grew and anastomosed freely with other hyphae. The cells, as in the other cases, were filled with fatty globules, when they ceased to grow, and gradually assumed a brownish colour. Fig. 24 represents one of these trichogyne-like processes in a culture which has been kept for about four months.

It must be noted here, that in all the cultures, in which these abnormal hyphae appeared, an abundance of perithecia were also formed on the main hyphae in the manner already described.

Though there are great differences in appearance and mode of growth between these abnormal hyphae and the hyphal clusters observed by Brefeld[1] on the mycelium of *Peziza tuberosa*, it is certain that they were alike produced under similar stimuli,—the presence of plentiful nourishment, and of a solid impenetrable substratum.

Whatever the function of these abnormal bodies may be under such a circumstance, one cannot help recalling, on seeing these hyphae in a young growing stage, some of the sexual organs represented in other groups of Ascomycetes. So striking is the resemblance between them, that I venture to suggest that under undue stimuli the hyphal branches of this fungus might have produced by reversion traces of their long-lost character, which became useless and disappeared on the acquisition of the power of the purely non-sexual formation of its perithecia.

Recapitulation of the principal results obtained.

1. The ascosporous stage of *Macrosporium parasiticum*, Thüm., is the common *Pleospora herbarum* (Pers.), Rabenh.

2. *Macrosporium parasiticum*, Thüm., is identical with *Macrosporium Sarcinula*, Berk.

3. *Pleospora herbarum* is decidedly a facultative parasite.

[1] O. Brefeld, Untersuch. üb. Schimmelpilze, Heft 4. p. 112. t. ix. Fig. 15 a, b. 1881.

4. There are only two stages in the development-cycle of *Pleospora herbarum*, the ascosporous stage and the *Sarcinula*-stage.

5. The presence of pycnidia in *P. herbarum* is very doubtful, and they may have entirely disappeared from its cycle of development.

6. An *Alternaria*-form does not belong to *P. herbarum*.

7. The formation of the perithecium is purely non-sexual.

8. No Woronin's hyphae or similar spiral processes are found in the perithecia before the formation of asci and paraphyses. The asci and paraphyses are produced from the same short chains of parenchymatous cells, which are formed by elongation and division of the pre-existing cellular group of parenchymatous nature filled with highly refractive contents, and situated generally in a central portion of the perithecium.

In conclusion, I wish to express my thanks to Prof. W. G. Farlow, who has helped me throughout my work with valuable suggestions, and allowed me also to make a free use of his library and collection.

The Cryptogamic Laboratory of Harvard University,
Cambridge, Mass., U.S.A., *July* 20, 1888.

EXPLANATION OF FIGURES IN PLATES I AND II.

Illustrating Mr. Kingo Miyabe's paper on the Life-history of *Macrosporium parasiticum*, Thüm.

PLATE I.

Fig. 1. A tuft of fertile hyphae of *Macrosporium parasticum*, Thüm., on the Bermuda onion-plant, showing the manner of their protrusion through its stomata. *a*, young hypha; *b*, swellings at base; *c*, swollen basidium; *d*, old basidium; *e*, old cup-shaped one; *f*, matured spore. × 400.

Fig. 2. Optical section of a matured spore of the same. × 500.

Fig. 3. An old fertile hypha of the same, showing a series of renewed growths of spore-bearing cells. × 400.

Fig. 4. A spiral formation of a very slender and transparent hyphal branch, formed on the mycelium of *Macrosporium*-spores sown in water. *a*, portion filled with fatty matters; *b*, spiral portion. × 800.

Fig. 5. Process of formation of the spores by abstriction. *a*, young fertile hypha before abstriction; *b*, after abstriction, basidum-portion growing; *d*, the spore dividing, and the wall of the basidium considerably thickened × 400.

Fig. 6. Twin-spores, the spore *a* formed later. × 400.

Fig. 7. Youngest stage of a perithecium formed on the mycelium of the *Macrosporium*-spore. *a*, initial cells; *b*, hyphal branches. × 500.

Fig. 8. A similar perithecium more advanced. × 500.

Fig. 9. A similar one still more advanced. × 500.

Fig. 10. Diagrammatic longitudinal section of the perithecium. *a*, darkened outer layer of cells; *b*, closely united parenchymatous wall; *c*, papilla; *d*, basal cells of asci and paraphyses; *e*, young asci; *f*, paraphyses.

Fig. 11. Young paraphyses, *p*, and their basal cells, *b*. *A*, young basal cell, forked. × 500.

Fig. 12. *A*, a young ascus; *n*, nucleus; *v*, vacuole; *p*, paraphyses; *b*, basal cells, *B*, one with very young spores, still colourless. *C*, somewhat advanced, spores with a light yellowish colour. × 500.

Fig. 13. Ripened ascus obtained by sowing the *Macrosporium*-spore. × 440.

Fig. 14. Ripened ascus from the specimen of *Sphaeria herbarum*, Pers., in Wartmann and Schenk, Schweiz. Krypt. n. 322. × 440.

Fig. 15. Unripened ascus from the specimen of *Pleospora Allii*, Ces. et de Not. in Herb. Critt. Ital., Ser. II. n. 644. × 440.

Fig. 16. Fertile hyphae, *a*, and conidial spores, *b* and *c*, of *Macrosporium parasiticum*, Thüm., from the authentic specimens in Myc. Univ. n. 667. × 400.

PLATE II.

Abnormal hyphae formed on the mycelium of *Pleospora herbarum*, in Van Tieghem cell-cultures. Figs. 17–23 obtained by sowing *Sarcinula*-spores.

Fig. 17. One drawn on Feb. 14, 4.25 P.M. × 500.

Fig. 18. The same on Feb. 16, 3.30 P.M. × 500.

Fig. 19. A similar process in the same culture, Feb. 15, 10 A.M. × 800.

Fig. 20. The same on Feb. 16, 10 A.M. At *c*, another spiral-process was formed. × 500.

Fig. 21. The spiral-process *c*, of Fig. 20, highly magnified.

Fig. 22. The same arrangement on Feb. 18, 12 M. From the spiral *c*, two stout branches were formed. × 500.

Fig. 23. One of simpler nature. × 500.

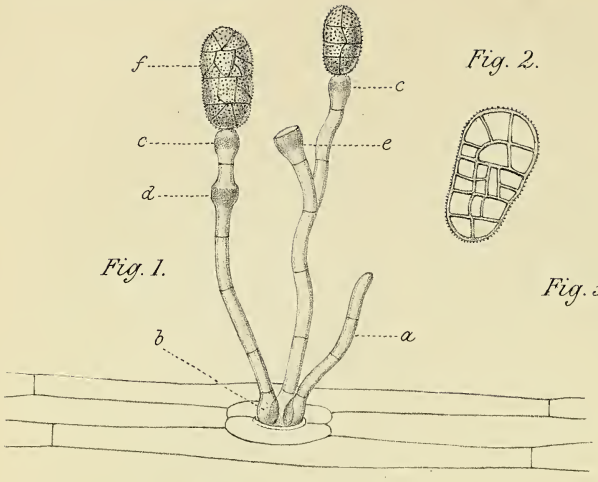
Fig. 24. A trichogyne-like process formed on the mycelium of the ascospores of *Pleospora herbarum*, drawn after having been kept for about four months in the culture. *a*, fatty globules. × 500.

APPENDIX.

The material studied by Mr. Miyabe was sent to me by the Rev. George Tucker of Smith's Parish, Bermuda. I visited Bermuda in January 1882, and at that time the onions were free from disease; but in 1886 I received a letter from Mr. Tucker, saying that a serious disease had attacked the onions, and he forwarded some diseased plants soon afterwards. I had expected that I should find either *Peronospora Schleideniana* or the *Urocystis* common on onions in the United States; but to my surprise no trace of either was seen. I noticed there was an abundance of *Macrosporium parasiticum*, Thümen. Early the following year more material was sent by Mr. Tucker, and, although a very large number of specimens was examined, with the rare exception mentioned by Mr. Miyabe, there was no trace of the *Peronospora*, a species readily recognised by its conidia, oospores, and characteristic mycelium. As in the material of the preceding year, the diseased plants were covered with *Macrosporium*. As *Peronospora Schleideniana* certainly does produce a serious disease of onions in Bermuda, as has been shown by Mr. Arthur E. Shipley, who visited Bermuda in 1887 for the purpose of studying the subject[1]; and as, with a rare excepiton, all of the numerous specimens of diseased onions from Bermuda which I had examined with great care showed no trace of *Peronospora*,—the question naturally arose whether the *Macrosporium* was merely a fungus which had attacked plants previously suffering from *Peronospora*, as most botanists would suppose, or whether it might not of itself cause a disease of onions. It was for the purpose of settling this point, if possible, that Mr. Miyabe, at my suggestion, undertook his investigation from which the possibility that *Macrosporium* can grow on the tissues of living plants free from *Peronospora* seems to have been demonstrated. I should here like to express my thanks to Mr. Tucker for the material which he kindly furnished.

W. G. FARLOW.

[1] Kew Bulletin of Miscellaneous Information, No. 10, Oct. 1887; also Proc. Camb. Phil. Society, vol. vi. Part 3 (1887).



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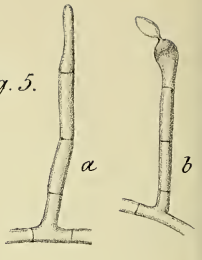

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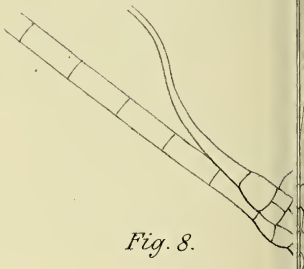

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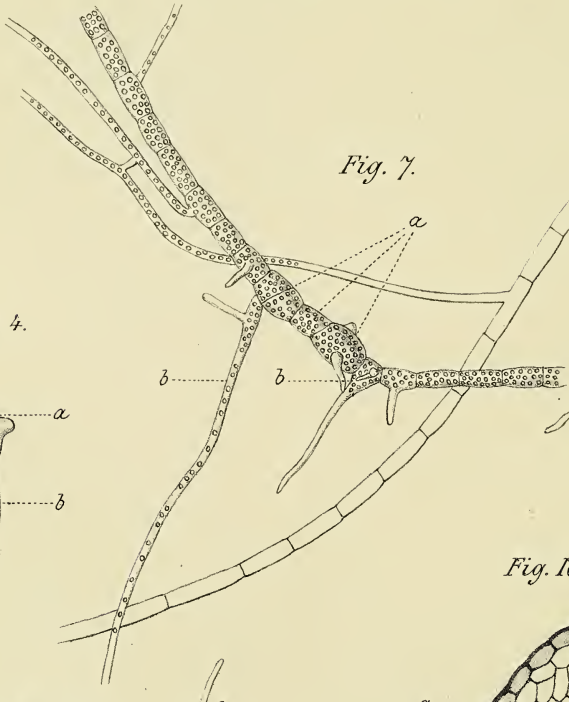

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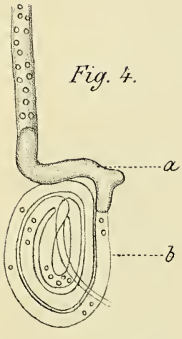

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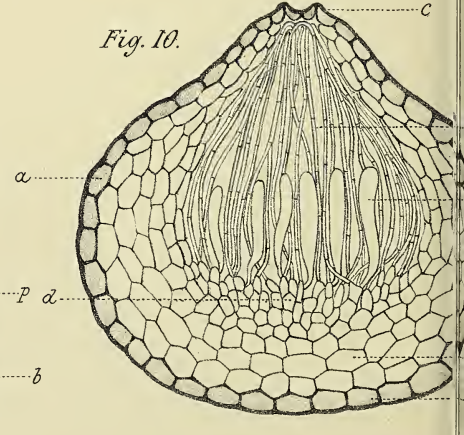

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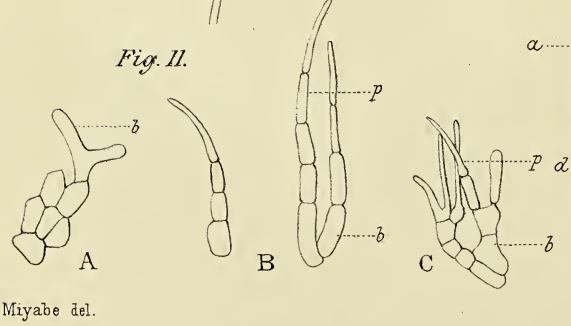

Fig. 11.

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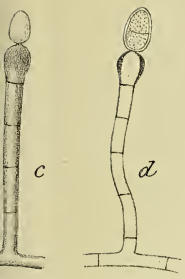
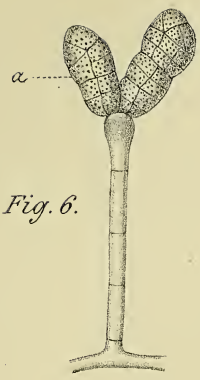
MIYABE.— ON MACROSPORIUM PARASITICUM, Thüm.





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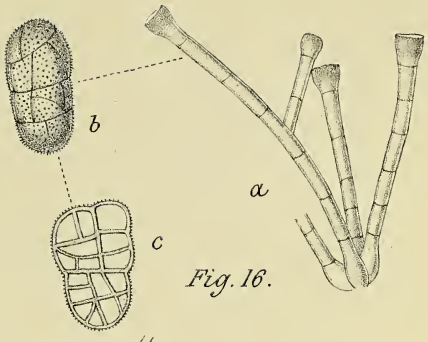

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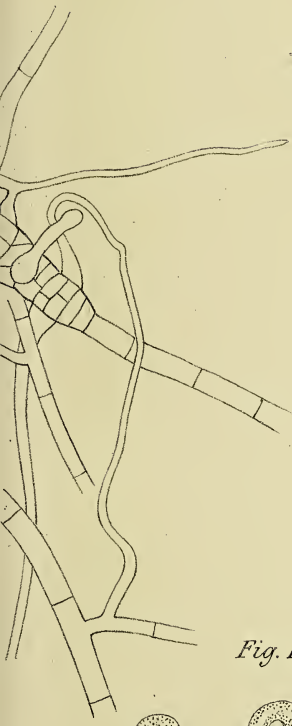

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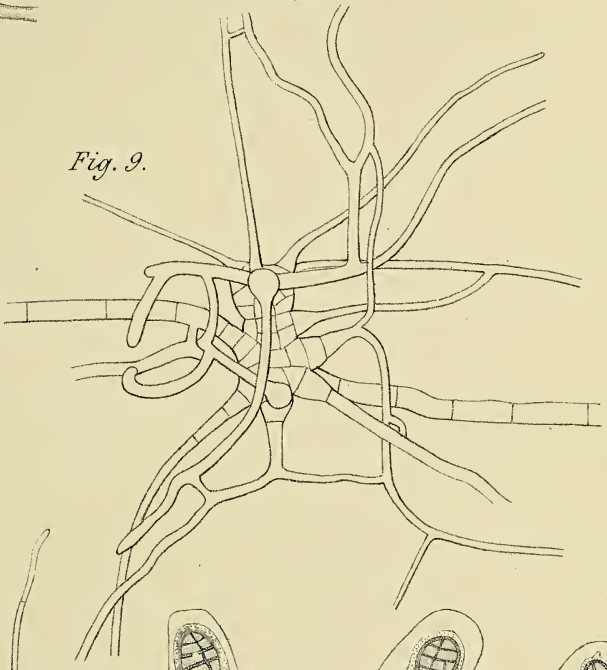

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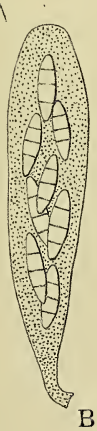

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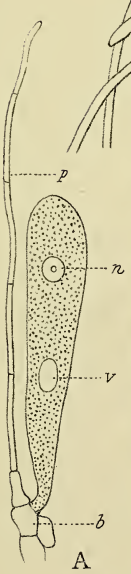

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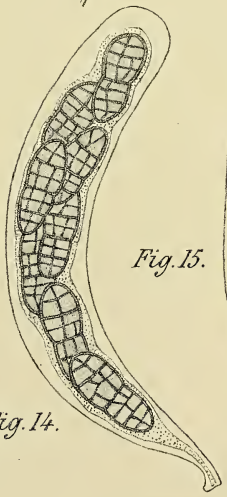

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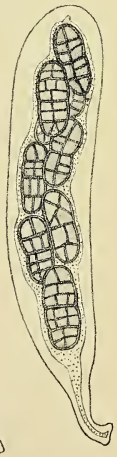

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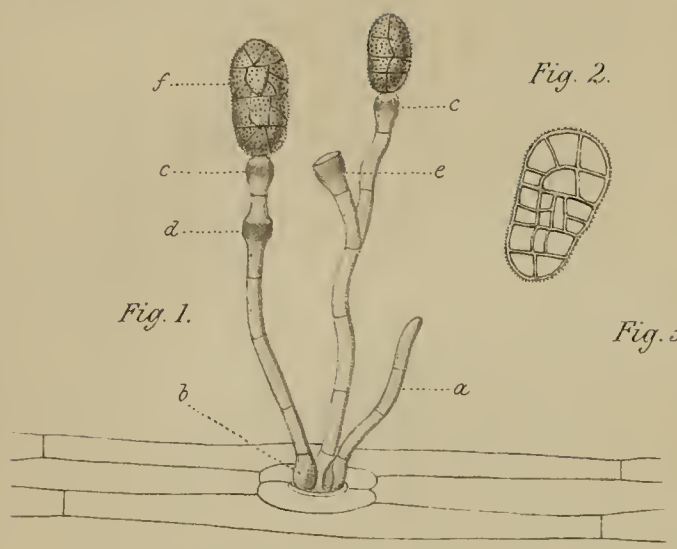

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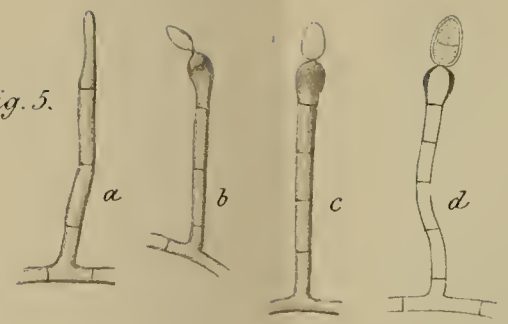

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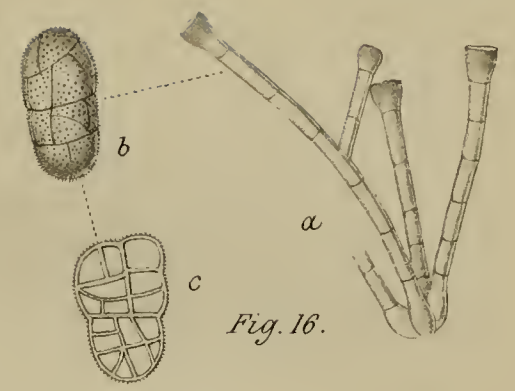

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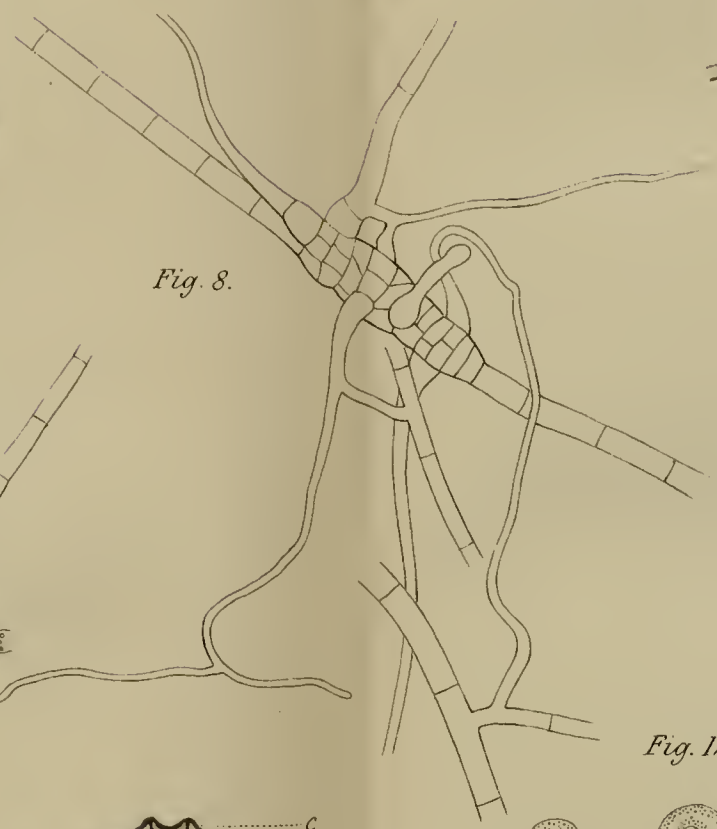

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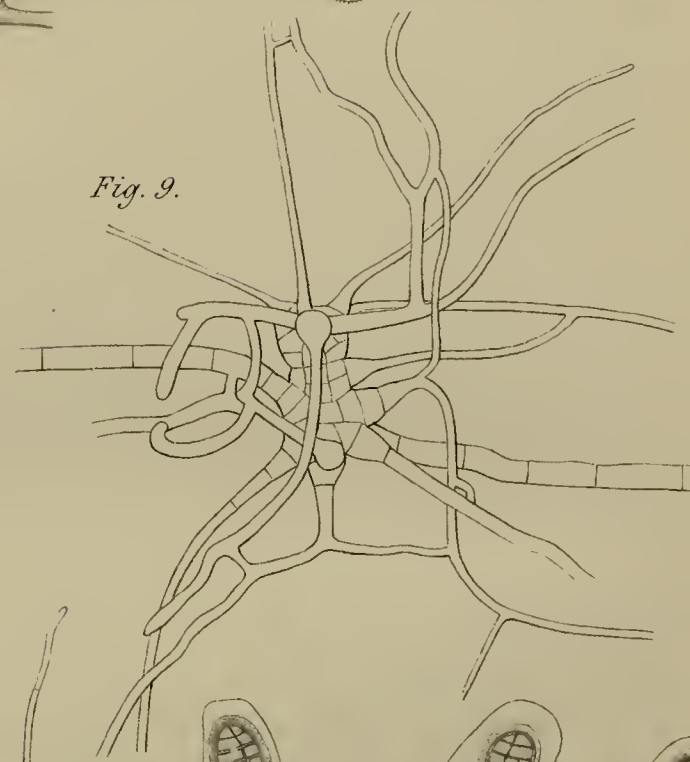

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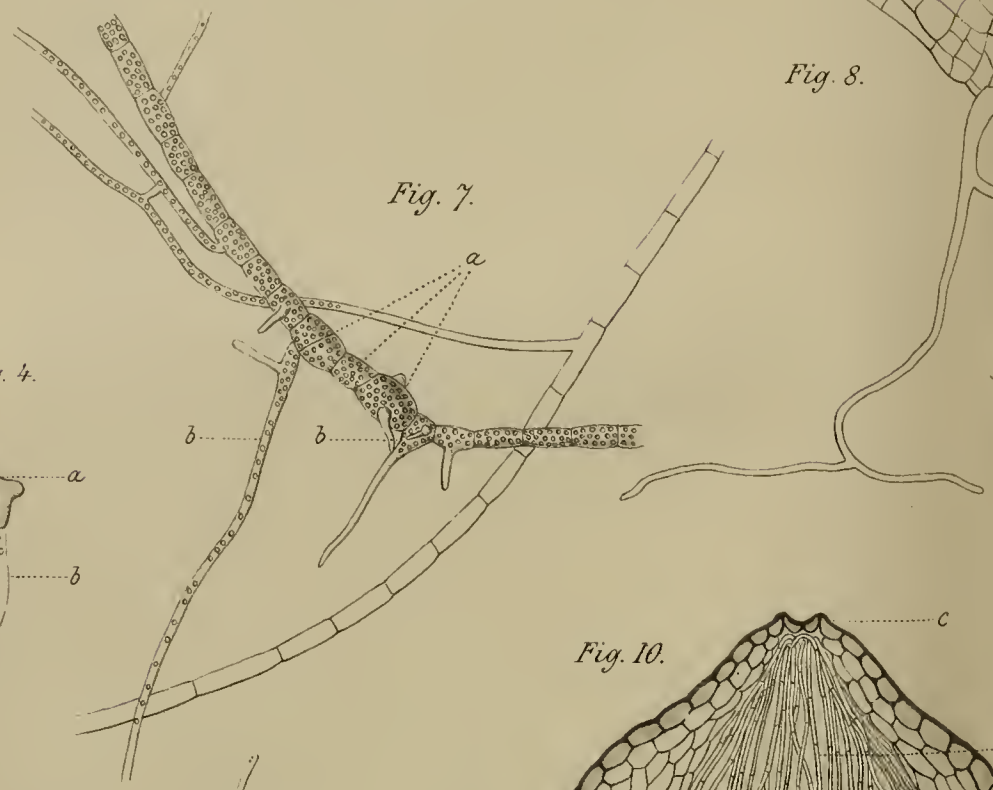

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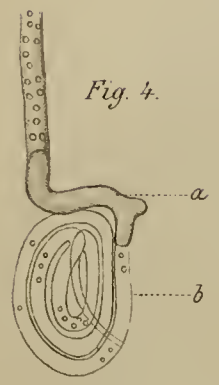

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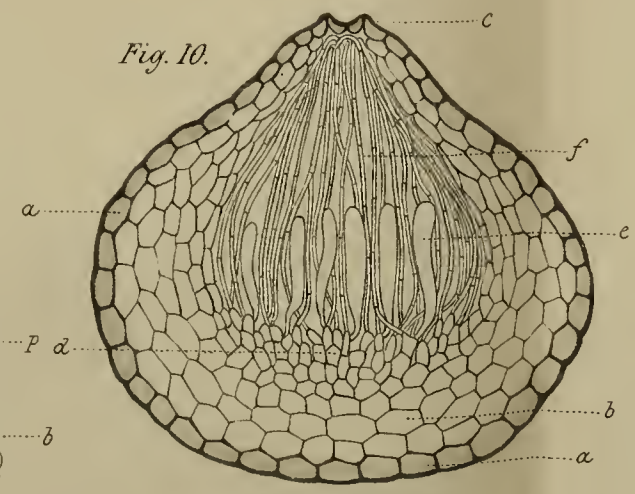

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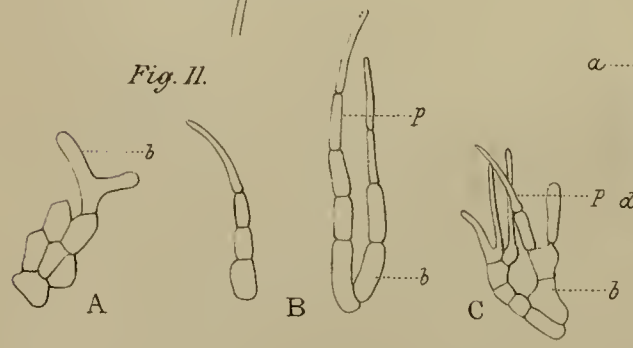

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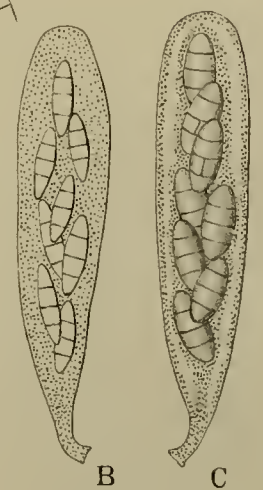

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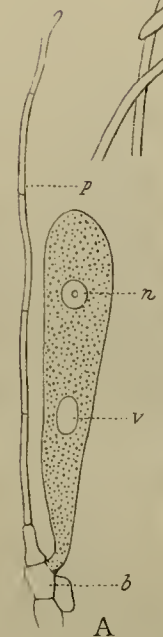

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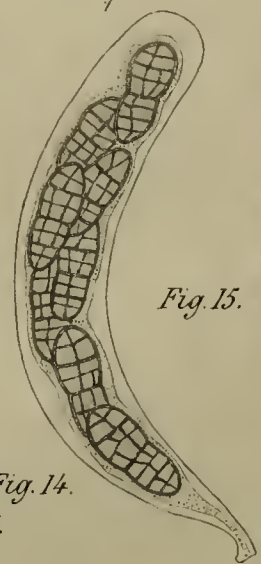

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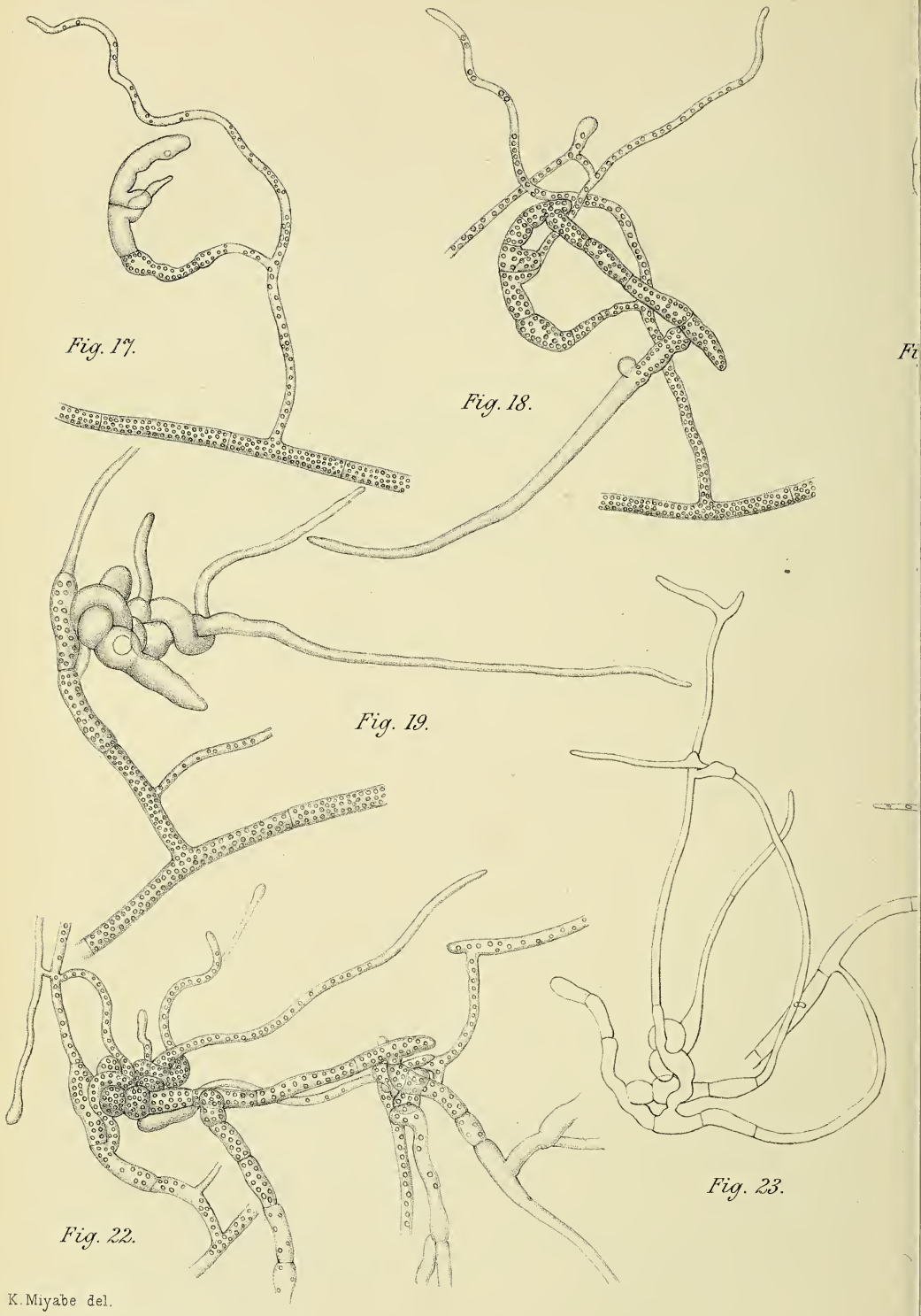

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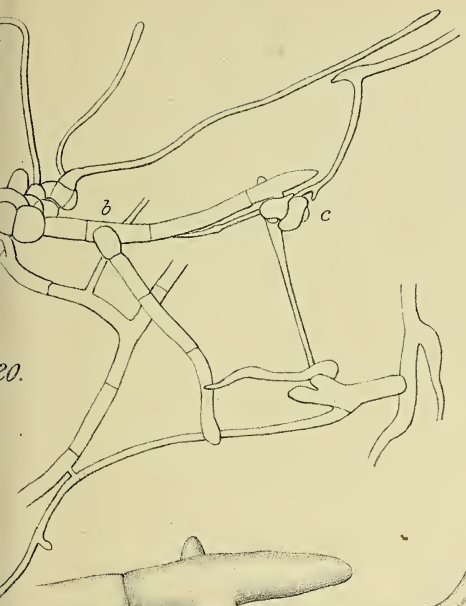

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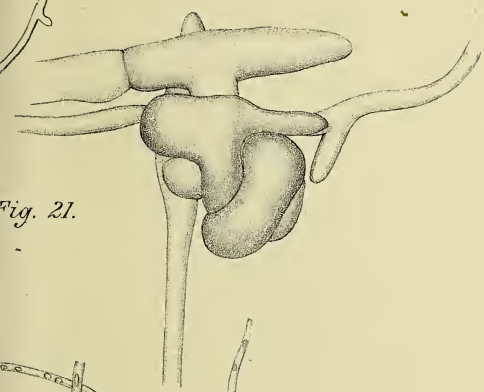

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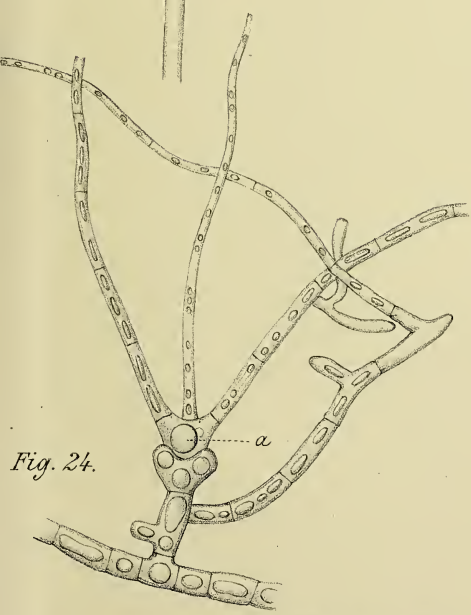

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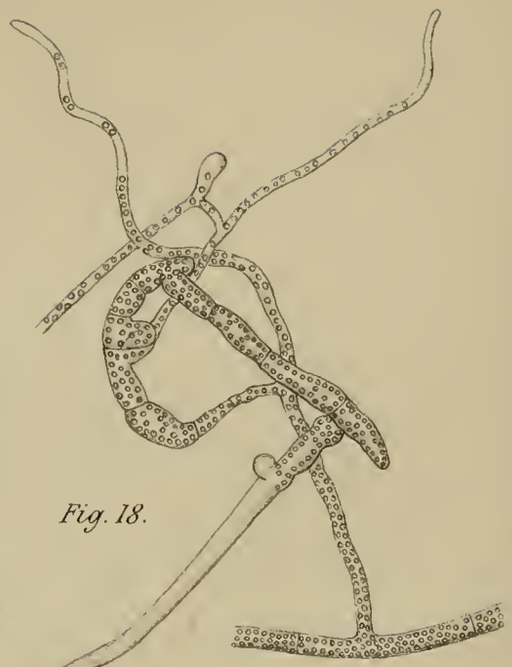

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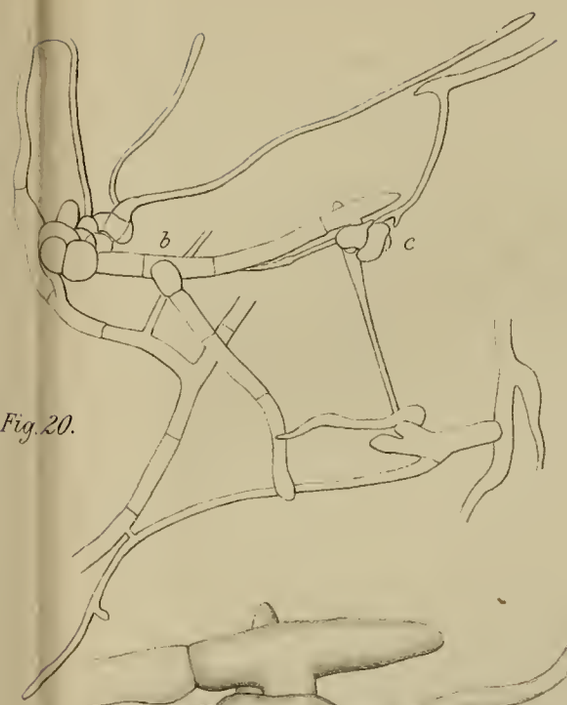

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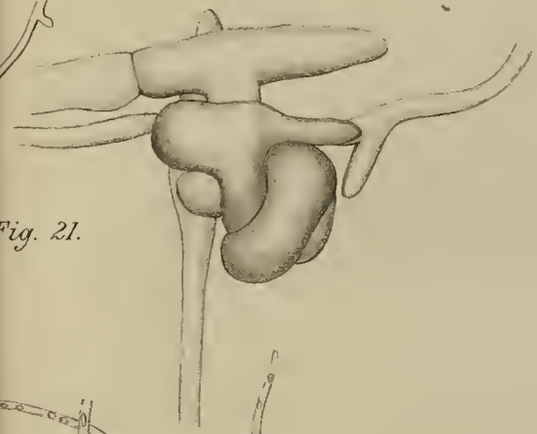

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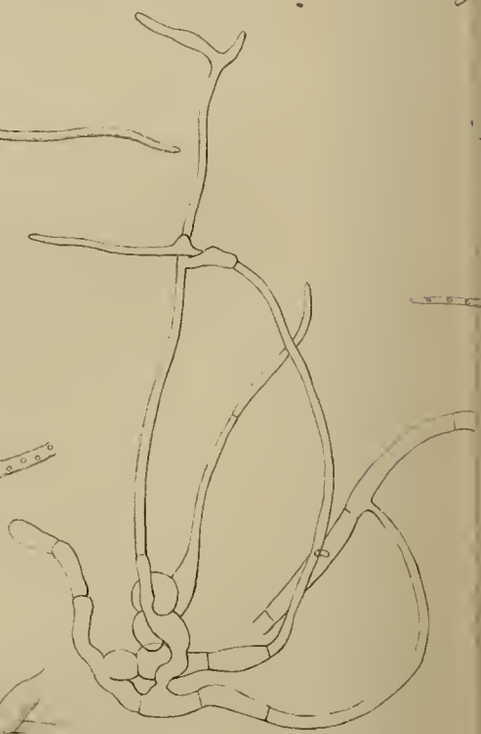

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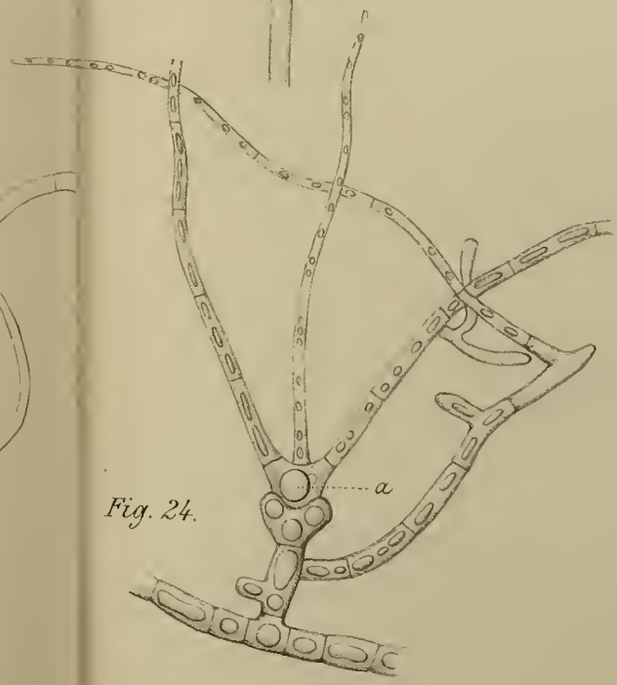

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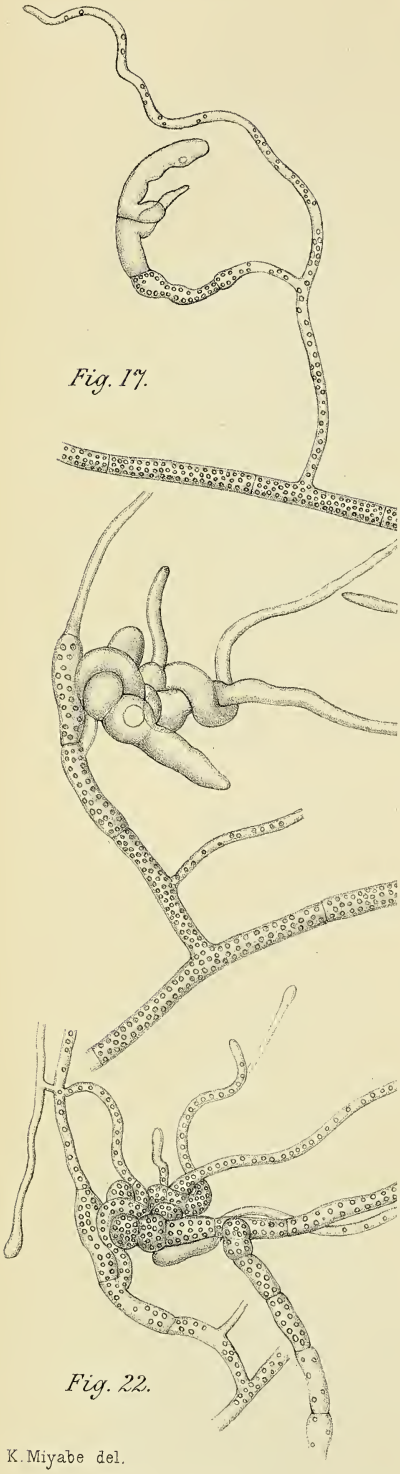

Fig. 17.

Fig. 22.

K. Miyabe del.

Abnormal Ferns, Hybrids, and their Parents[1].

BY

E. J. LOWE, F.R.S.

AND

COLONEL JONES.

With Plate III.

WE do not intend by anything said in this paper to ignore the exertion of others in the same field; we only wish to place on record our personal experience, and what we have accomplished by the labour of a number of years.

More than thirty years ago experiments were commenced, and twenty-one years ago a paper was read by one of us (Mr. Lowe) 'on hybrid ferns' at the Dundee Meeting of the British Association. The subject was at that time in its infancy, and none of the botanists then present, with the exception of the late Professor Balfour, thoroughly believed in these crosses. The next year, 1868, the Rev. M. J. Berkeley sent a paper on the supposed crossing of two American species to the Royal Horticultural Society, and the late Sir William Hooker remarked 'that it was the most probable instance he had yet met with of a real hybrid amongst ferns.' This was a hybrid between *Camptosorus rhizophyllus* and *Asplenium ebeneum*.

The late Mr. Clapham, who had given the subject careful investigation for some years, only became convinced by seeing

[1] Read in Section D, British Association, on September 10th, 1888.

[Annals of Botany, Vol. III. No. IX, February 1889.]

in 1879 the series of examples Mr. Lowe was taking to the British Association at Sheffield,—crosses of varieties of *Athyrium*, in which were spores of *Victoriae* and *Proteoides*.

Afterwards, about fifteen years ago, endeavours were made by one of us (Mr. Lowe) to cross *Polystichum aculeatum* with *Polystichum angulare*, and when the seedlings had become mature (seven years afterwards), it was apparent, at all events to the experimenter, that this cross had been accomplished, but in only five examples out of 1000 seedlings. The object was to obtain a narrow cruciate variety of *Polystichum aculeatum*, a copy in *Polystichum aculeatum* of the narrow cruciate variety *Wakeleyanum* of *Polystichum angulare,* for as yet this was a desideratum. *Polystichum angulare*, variety *Wakeleyanum* (Fig. 1), was sown together with a dense-fronded variety of *Polystichum aculeatum*, known as *densum* (Figs. 2). In 1884 a specimen of this hybrid and a short paper were sent to the Linnean Society, but this was not sufficient to remove the doubts of botanists; a year later, however, a letter from Sir Joseph Hooker stated that the crossing of ferns was then an acknowledged fact. This hybrid (Fig. 3), and its parents, together with some of the offspring of the hybrid, were last year exhibited at the Bath Floral Fete, amongst the specimens of botanical interest, and it was awarded a first-class certificate.

Both of us have had great experience in the crossing of ferns, one of us (Colonel Jones) starting a little later than the other, and our results coincide. Instances of crossing have now accumulated to such an extent as to preclude the possibility of any further doubt on the subject. To produce the results, however, great care is necessary that the germinations of the spores are very general and also simultaneous. The clear proof of the reality of the crossing of varieties lies in the fact of the production of plants, either bearing a character intermediate between those of the plants sown, or combining their characters.

A remarkable fact in connection with the crosses is the frequent transference of the character of one variety to another, this even applies to variegation. It will be seen in the example of the cruciate hybrid of *Polystichum aculeatum*,

that it is a marked copy of the cruciate form of *P. angulare*, one of the parents selected with the object of obtaining a cruciate *P. aculeatum*. Instead of the usual gradual process, the form was obtained at once. This applies equally in the case of the polydactylous forms of *P. angulare* (see Figs. 4, 5, and 6), and in the variegated forms of *Scolopendrium vulgare*.

As example, we have selected experiments made with varieties of *Athyrium* and *Scolopendrium* from Mr. Lowe's series, and some made with varieties of *Polystichum* from Colonel Jones's series. We might have given several hundred examples, but a few of each is ample illustration.

Example 1. ATHYRIUM.

The following varieties were sown together: *Victoriae*, *multifidum*, *Jonesii*, *Craigii*, *uncum*, *Harrisae*, *cruciatum*; *Proteoides*, *tortile*, *reflexum*, *laciniatum*, and *grammicon*.

The result has been several hundred intermediate forms, some very interesting.

Example 2. SCOLOPENDRIUM.

In this experiment the varieties were *crispum* (rarely fertile); *Victoriae*, *muricatum*, *marginatum*, *undulatum*, *digitatum*, *ramo-cristatum*, *laceratum*, and a variegated *crispum*.

The result has been various intermediate forms, a number of which are variegated; for instance, the variegation in the *crispum* has passed into a crested form, the colour as well as the shape being altered.

Example 3. POLYSTICHUM.

The attempt was made to transfer the polydactylous character of certain forms of *P. angulare* to other forms of the same species, which preserved the normal outline and distinct individuality, but were not polydactylous.

The forms used were Mr. Padley's polydactylous form from the Vale of Avoca, and Colonel Jones's Hampshire form. The polydactylous character has now been successfully transferred to the forms known as *decompositum*, *acutilobum*, *divisilobum*,

frondosum, *alatum*, *lineare*, *congestum*, *inaequale-variegatum*, and others. The polydactylous character of *P. angulare* has also been transferred to *P. aculeatum*.

There are now four clearly established cases in which the characters of distinct forms of *P. angulare* have been transferred to *P. aculeatum*. Hitherto the varieties of *P. aculeatum* have been very few, so that now a new field for exertion is open, the results of which it is difficult to overestimate, for the robust constitution of *P. aculeatum* enables it to thrive in climates in which *P. angulare* would soon perish.

The interest in the varieties of British Ferns ought to increase now the crossing of varieties has become an acknowledged fact, alike on account of the extreme beauty of many of the crosses already effected, and also because, however beautiful crosses already obtained are, it may be confidently asserted that they are nothing to what will be accomplished when exhaustive experiments, guided by tasteful and judicious selection, shall have been made. Though much will depend on selection, there will always be enough left to the element of chance to keep up the interest. We may liken the prospect of endless combinations to the combinations in bell-ringing, and we learn that the changes in the ringing of twelve bells amount to forty millions. We can scarcely conceive of the immense field of inquiry that is opened up in these investigations. The number of forms to be obtained is past all conception, and as the discovery of one truth is the stepping-stone to the discovery of even greater truths, so every new form that is raised, enables the raiser or those following in his footsteps to produce countless other combinations.

EXPLANATION OF FIGURES IN PLATE III.

Illustrating Mr. Lowe's and Col. Jones's Paper on Abnormal Ferns, Hybrids, and their parents.

Fig. 1. *Polystichum angulare*, var. *Wakeleyanum*. Parent.

Fig. 2. *Polystichum aculeatum*, var. *densum*. Parent.

Fig. 3. *Polystichum aculeatum*, var. *cruciatum*. Hybrid between preceding Figs. 1 and 2.

Fig. 4. *Polystichum angulare*, var. *polydactylum*. Parent.

Fig. 5. *Polystichum angulare*, var. *multilobum*. Parent.

Fig. 6. *Polystichum angulare multilobum*, var. *polydactylum*. Hybrid between preceding Figs. 4 and 5.

Fig. 1.

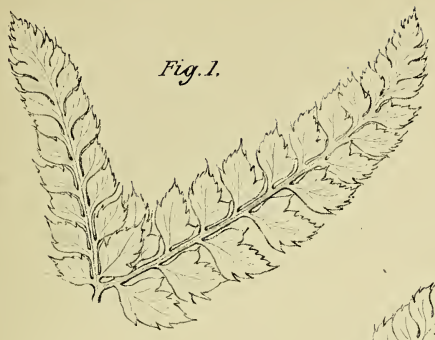

Fig. 3.

Fig. 2.

Fig. 5.

Fig. 4.

Fig. 6.

A. M. Jones del.

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LOWE AND JONES.— ON HYBRID FERNS.

A New Development of Ephelis.

BY

DR. M. C. COOKE

AND

GEORGE MASSEE.

With Plate IV.

THE genus *Ephelis* of Fries has throughout been involved in mystery. In 1849 a short diagnosis appeared in the 'Summa Vegetabilium Scandinaviae,' where it was included under Discomycetes, near *Rhytisma*, but the description did not determine its affinity:—'Perithecium (stroma) crustaceo-effusum, hinc inde tuberculosum, tuberculis in excipula cupularia dehiscentibus;' the presence of asci seems not to have been determined. In 1869 Berkeley included the genus in his Cuban Fungi as an ally of *Sphaeropsis*, with Fries's original species, there called *Ephelis mexicana*; and in 1875 another species was added from Ceylon as *Ephelis brevis*, B. & Br. In the Berkeley Herbarium is a specimen from Fries, inscribed by his own hand '*Ephelis typhina*, Fries,' from Mexico, and with it the Cuban specimens, there called *Ephelis typhina*, but described by Berkeley under the name of *Ephelis mexicana*. Undoubtedly all are the same species, and as we do not find any diagnosis of *Ephelis typhina*, the later name of *Ephelis mexicana* will stand. These specimens are stylosporous, and correspond with the description in Saccardo's Sylloge, vol. iii. No. 3645, having spores about 25 μ long. Subsequent to the publication of the last-named work, Mr. Phillips[1] has appropriated the genus *Ephelis* as an ascomycete, although there is no evidence that Fries intended, or suspected, anything of the

[1] Manual of British Discomycetes, p. 358.

kind, notwithstanding his placing it under Discomycetes, any more than he suspected *Leptostroma*. This is another unfortunate illustration of the mistake of appropriating old genera, retaining the name, but amending the diagnosis. *Ephelis Rhinanthi*, of Phillips, therefore is not congeneric with the *Ephelis mexicana* (or *typhina*), Fries, which has its place correctly assigned in Excipulaceae, a family of Sphaeropsideae.

Recently Mr. J. H. Hart of Trinidad sent to the Kew Herbarium some specimens of *Panicum palmifolium*, strangely metamorphosed by a parasitic fungus, which, upon examination, was found to agree entirely with the genus *Ephelis* of Fries, and indeed very nearly with the type species *Ephelis mexicana*. As in other cases of proven dimorphism, the stylosporous form and the ascigerous form have still been retained separately under their respective genera; so in this case, although not autonomous, as will hereafter be seen, the *Ephelis*-form deserves a place beside the other species in that genus, under the name of—

Ephelis trinitensis, Cooke & Massee.

Stroma solido, nigro, effuso, circumambiente, typhoideo; receptaculis pezizoideis, erumpentibus, ellipticis, margine lacerato, hymenio griseo, sporulis filiformibus continuis, rectis vel leniter curvulis, hyalinis (25–30 × 1·5 μ) basidiis brevibus suffultis.

On inflorescence of *Panicum palmifolium*.

Had no further specimens been collected, it would have been assumed that the above was the complete development of this curious fungus, but, fortunately, other specimens were secured afterwards on the same host, and upon the same estate, which carried the history forward much further. Instead of the discoid, cup-like receptacles, exhibited by *Ephelis*, each of them was transformed, or was in the course of a transformation into a depressedly globose capitulum of 1 to 1½ mm. diameter, raised upon a peduncle two or three times that length; the transformation being brought about by the replacing of the concave surface of the cups by a convex one

and the subsequent elevation of this surface on a stalk. This was practically the production of a secondary capitate stroma from the effete discs of the old effused stroma, each one having somewhat the appearance of enlarged specimens of *Claviceps purpurea*, nearly black in colour all over, the stem being squamulose, and the capitulum enclosing immersed membranaceous perithecia, containing asci with long filiform ascospores. No doubt could be entertained that this new form had its affinities in the Hypocreaceae, and was a sort of gregarious *Claviceps* seated upon a continuous effused stroma.

There is very little doubt the fungus in question must be referred to a new genus called *Balansia*, of which one species only, and that from South America, has been described under the name of *Balansia Claviceps*, Speg. This genus differs from *Claviceps* in the capitate stroma, being developed from the effete discs of the *Ephelis*, which were themselves developed from a circumambient stroma of quite a different character from the sclerotioid base of *Claviceps*. It differs also from *Epichlöe* in the perithecia not being immersed in the ambient stroma, but in secondary capitate stromata which spring from determinate points in the effused stroma. Altogether the structure and history is a complex one, and must be studied from the figures and details hereafter given, when it will be manifest that the species could not have been included either in *Claviceps*, *Epichlöe*, or *Hypocriella*, the nearest allies.

As to the species itself, it differs in such important particulars from *Balansia Claviceps*, Speg., that we do not think it could be maintained as a mere variety of that species. The following is a technical description :—

Balansia trinitensis, Cooke & Massee.

Stromatibus globulosis, subtus impressis (1–1½ mm. diam.), duris, atris, extus papillatis. Stipite erecto, *squamuloso* (2–4 mm. long, ½ mm. crass.), atris. Peritheciis in stromatum capitulis peripheriis, constipatis, obovatis, ostiolo exiguo perforato, Ascis cylindraceis, basi attenuatis (120–130 × 9–10 μ), octosporis, sporidiis filiformibus, continuis, flexuosis, hyalinis

(90–100 × 1½ μ). Stroma conidiifera = *Ephelis trinitensis*, Cooke & Massee.

On inflorescence of *Panicum palmifolium*, from Trinidad. Com. J. H. Hart.

The above will be seen to differ from *Balansia Claviceps*, Speg., as described by Saccardo [1], in the following points :—

1. In its development from the effete discs of a species of *Ephelis*, of which it appears to be the ultimate and ascigerous condition.

2. In the stems of the capitate stromata being distinctly squamulose ; and

3. In the smaller size of the asci and ascospores.

Externally there is very little difference in the appearance of the two species, and in the manner in which the spikes of the grass are deformed ; but the association of the ascigerous fungus in such an intimate manner with an *Ephelis*, seems to warrant either the description of a new species, or the modification of the diagnosis of the previous one to an extent which could certainly not be justified without the consent of the author. M. C. Cooke.

Morphology.

The inflorescence of *Panicum palmifolium* is a loose panicle from 14–18 cm. long, and when attacked by the fungus is converted into a rigid, black, simple spike, about 4 mm. thick (Fig. 1) ; sometimes one or two of the lower branches remain free, although attacked by the fungus (Fig. 1 *a*, *a*). Owing to the material arriving in a dried condition, and for the most part fully developed, but little can be ascertained respecting the earliest stages of development. The stroma of the fungus is formed while the inflorescence is yet surrounded by the leaf-sheath, with its branches closely appressed to the main axis, and in all probability the young flowers are first attacked, from which the hyphae extend in all directions, and form a continuous felt-like sheath enclosing the branches and main axis of the inflorescence, a transverse section presenting the appearance of a stem with scattered vascular

[1] Sylloge Additamenta, p. 220.

bundles (Fig. 3). The stroma consists of a compact, colourless, uniform, pseudo-parenchymatous tissue, surrounded by a blackish rind or cortex. The hyphae of the central portion are frequently branched, aseptate, or with only an occasional septum, thick-walled, and with small lumina, and as they pass to the outside to form the cortex become thin-walled, dark-coloured, and furnished with numerous septa. The greater part of the surface of the cortex is smooth, but here and there some of the dark cortical cells continue to elongate beyond the general surface, and form velvety patches (Fig. 3, *c*). It is remarkable how comparatively few hyphae are to be met with in the tissues of the main axis or branches of the host, there being no displacement of cells or general disintegration of the cell-walls; even the hairs on the surface remaining intact (Figs. 4, *d* and 5, *d*). The hyphae pierce the walls of the cells, and sometimes give off short, inflated branches, which probably act as organs of absorption (Fig. 4, *c*). The earliest external evidence of the *Ephelis* or gonidial stage of reproduction is indicated by the presence of numerous minute elevations scattered somewhat uniformly at short distances over the hitherto even surface of the stroma. A vertical section through one of the pustules at this stage shows the hyphae of the colourless portion of the stroma immediately below the cortex to be arranged more or less parallel and vertical to the surface for a depth of 20–30 μ. This mass of differentiated hyphae, which is biconvex in vertical section, continues to increase in size on the side next the cortex until the latter is eventually ruptured, forming an elliptical or irregularly circular opening from 1–2 mm. across. The margin of the ruptured cortex is raised in the form of a border surrounding the central exposed portion, and presents under a low power a fringed appearance, due to the component hyphae of the cortex becoming separated by the pressure from below, and standing erect round the torn margin (Figs. 5 and 8). The parallel hyphae forming the disc of the cavity consist at first of aseptate branched filaments, the apices of which are eventually abscised as con-

tinuous, filiform, colourless gonidia, measuring from 25–30 × 1·5 μ (Fig. 6). These gonidia under a magnifying power of 400 diameters present an appearance which might be mistaken for septation, but when more highly magnified is seen to be due to the presence of a single row of vacuoles (Fig. 7). There appears to be a considerable interval of time between the full development of the gonidia and the ascigerous condition which follows. The specimens collected by Balansa[1], from which the genus was established by Spegazzini[2], illustrate the ascigerous condition; hence the generic character is imperfect, inasmuch as the *Ephelis* stage is not mentioned. In the specimens sent from Trinidad by Mr. Hart, the two conditions are present. The secondary ascigerous stroma not unfrequently originates immediately below an old empty gonidial cavity, through which it bursts, and remains until the spores are mature as a sessile, spherico-depressed swelling, surrounded by the raised margin of the *Ephelis* (Fig. 9). When the ascigerous structure does not occupy an old gonidial cavity the earliest external indication of its existence is a swelling of the primary stroma, the cortex being eventually ruptured by the growth of the ascigerous stroma, round which it forms a raised pilose border exactly as in the gonidial condition. In some spikes nearly every ascigerous stroma occupies a gonidial cavity, whereas in others there is no evidence of the *Ephelis* stage having existed, the ascigerous condition bursting directly through the cortex of the primary stroma; in others, again, both modes of origin of the ascigerous stage are present.

The ascophore originates at some distance below the primary cortex as a spherical weft of intricately interlaced hyphae (Fig. 15), that appear to become directly differentiated on the side towards the cortex into the spherico-depressed head of the ascophore, which is umbilicate below, and furnished with a very short stem-like base, sunk in the umbilicus. The

[1] B. Balansa, Pl. du Paraguay, n. 253.

[2] Speg., Fung. Guaranit., Pug. I, n. 253; also in Sacc., Syll. Fung. Additamenta to Vols. I–IV, n. 7249.

hyphae forming the stem run mostly parallel in the direction of its length, are thick-walled, sparsely septate, and on entering the head diverge in a radiating manner towards the circumference, where they increase in thickness, are furnished with numerous septa, and form the cortex, which eventually becomes black (Fig. 16). The structure of the ascophore is at first uniform, and smooth externally; but before it bursts through the primary cortex a number of minute differentiated spherical coils of hyphae or primordia are formed at a short distance below the cortex. These primordia, the minute structure of which could not be determined from dried material, are the starting-points of perithecia, which, when mature are flask-shaped, with an elongated neck, opening by a definitely formed ostiolum through the blackened cortex, which is raised as a papilla; hence the surface of the mature ascophore is warted (Fig. 10). When mature the perithecia consist of a thin wall composed of very slender interwoven hyphae, sharply differentiated from the stroma in which they are imbedded, and filled with cylindrico-clavate asci measuring 120–130 × 10–12 μ (Fig. 12), each containing eight filiform, colourless, continuous sporidia 90–100 × 1·5 μ (Fig. 13). The stem of the ascophore remains rudimentary until the perithecia are completely formed, when it elongates until it reaches a length varying in different individuals from 3–4 mm. During the increase in length the axial portion grows at a greater rate than the peripheral, in consequence the cortical hyphae are ruptured, the free tips spreading and giving the stem a minutely scaly appearance (Fig. 10). The general structure of the ascigerous stroma agrees closely with that of *Claviceps purpurea*, as described and figured by Tulasne[1]; but in the latter the gonidial mode of reproduction differs considerably from what occurs in the plant under consideration.

GEORGE MASSEE.

[1] Mémoire sur l'Ergot des Glumacées. in Ann. Sci. Nat., sér. 3, vol. xx. p. 5, Pl. 1–4. Figures reproduced by De Bary in Biol. of Fungi, Mycetozoa and Bacteria (Engl. ed.), Fig. 108.

EXPLANATION OF FIGURES IN PLATE IV.

Illustrating Dr. Cooke's and Mr. Massee's paper on a new development of *Ephelis*.

Fig. 1. An inflorescence of *Panicum palmifolium* infested with *Balansia trinitensis*. *a a*, basal branches of the inflorescence infested with the fungus, but not adpressed to the main axis; the greater part of the fungus is in the early ascigerous condition; at *b*, the stem of the ascophore is becoming elongated. Nat. size.

Fig. 2. Portion of a spike with the ascosporous condition of the fungus fully developed. Nat. size.

Fig. 3. Transverse section of a diseased inflorescence. *a*, rachis of inflorescence. *b*, a branch of the inflorescence. *c*, stroma of fungus. *d*, cortex or rind of stroma. × 80.

Fig. 4. Transverse section through part of a diseased inflorescence. *a*, portion of branch. *b*, stroma of fungus. *c*, *c*, hyphae with lateral swollen branches. *d*, a hair on the branch. × 400.

Fig. 5. Vertical section through a gonidial disc (*Ephelis trinitensis*). *a*, gonidia. *b*, coloured hyphae forming fringed margin bordering the *Ephelis*. *c*, portion of a branch of the inflorescence. *d*, hair from epidermis of branch. × 400.

Fig. 6. Isolated gonidiophores. *a*, supporting gonidia. *b*, belonging to gonidial or *Ephelis*-stage of reproduction. × 400.

Fig. 7. Gonidia. × 1000.

Fig. 8. Gonidial or *Ephelis*-stage of reproduction. × 75.

Fig. 9. Young and yet sessile ascophore seen from above. × 75.

Fig. 10. Group of mature ascophores springing from gonidial cavities, *a*, *a*. × 75.

Fig. 11. Vertical section through an ascophore. *a*, capitate stroma with perithecia. *b*, persistent gonidiophores of the gonidial disc. *c*, remains of the primordium. × 400.

Fig. 12. Asci. × 400.

Fig. 13. Ascospores. × 400.

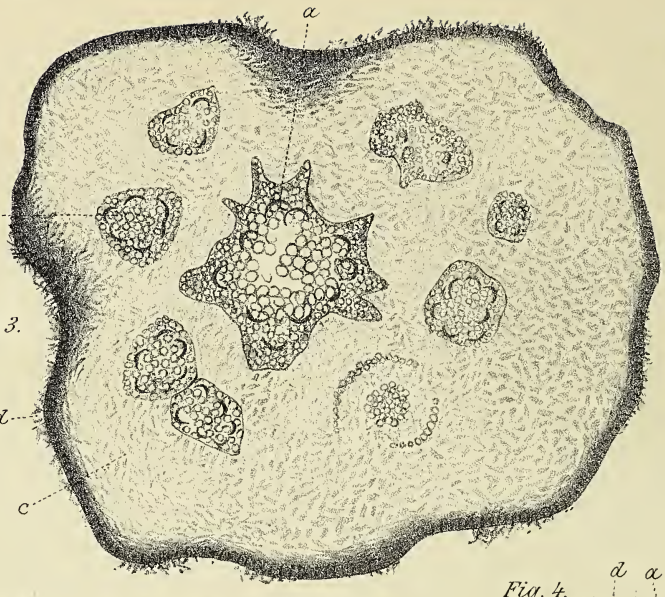
Fig. 14. Portion of an ascospore, showing the protoplasm broken up into separate pieces, which produces the appearance of septation under a power of 400 diam. × 1000.

Fig. 15. Vertical section through the primary stroma passing through an old gonidial disc with the permanent gonidiophore, *a*. *b*, young primordium of an ascophore. × 400.

Fig. 16. Hyphae from the capitate stroma of an ascophore which become thickened, closely septate, and brown towards the exterior. × 400.

Fig. 1.

Fig. 2.



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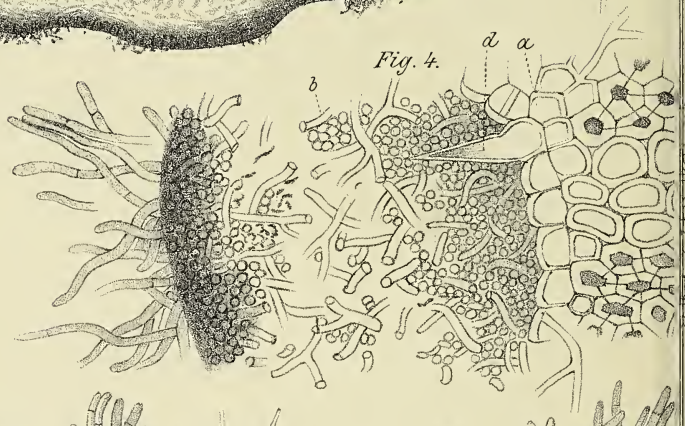

Fig. 4.

Fig. 5.

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COOKE & MASSEE.— ON EPHELIS.

Fig. 8.

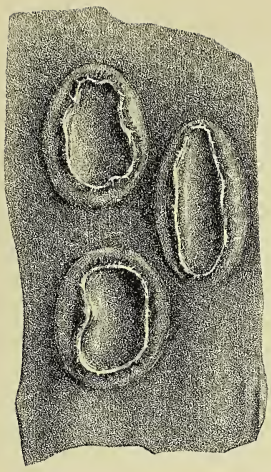

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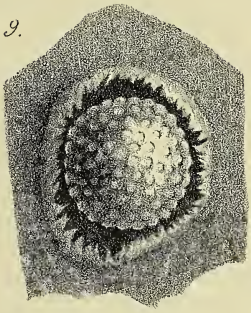
Fig. 6.

Fig. 16.

Fig. 10.

a

Fig. 9.



c

c

Fig. 11.

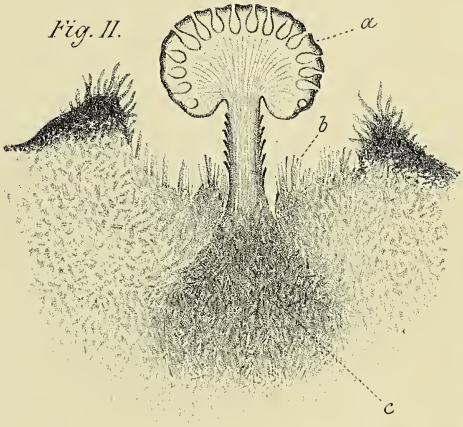


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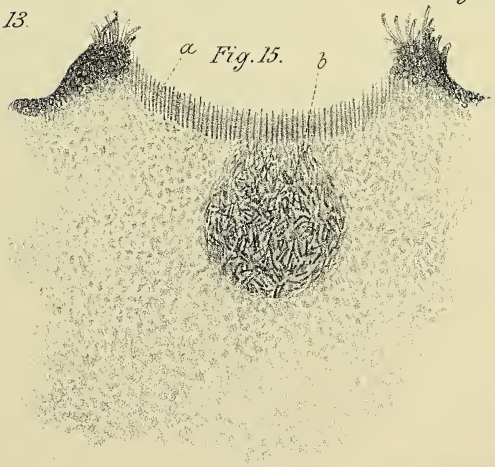
Fig. 12.

Fig. 13.

Fig. 14.



a

Fig. 15.

b

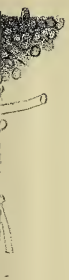


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Fig. 1.

Fig. 3.

Fig. 2.

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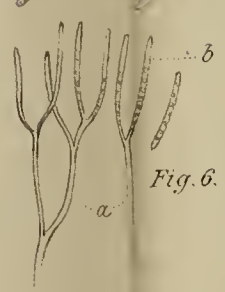

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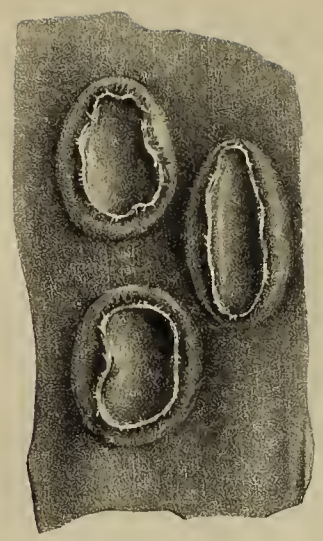

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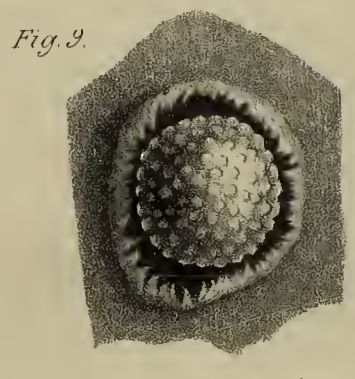


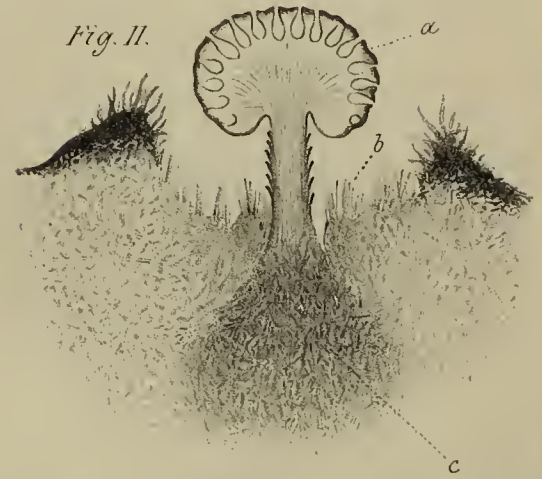
Fig. 9.

Fig. 12.

Fig. 13.

Fig. 16.

Fig. 10.



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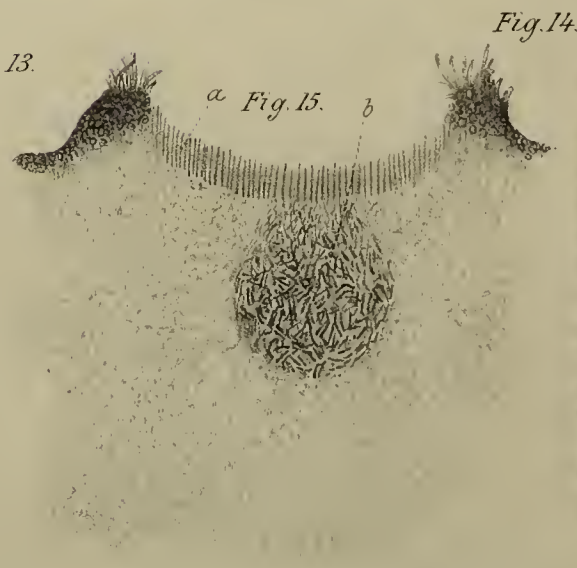

Fig. 15.

Fig. 14.

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COOKE & MASSEE.— ON EPHELIS.

On the Structure and Development of the Bulb in Laminaria bulbosa, Lamour.

BY

C. A. BARBER, B.A.,

Scholar of Christ's College, Cambridge.

With Plates V and VI.

Historical Introduction.

IN the proceedings of the Cambridge Philosophical Society for 1885 Mr. Walter Gardiner drew attention to the fact that *Laminaria bulbosa* bears 'sporangia upon its roots.' It was his intention at that time to describe the development of these so-called 'roots,' and material was collected for the purpose[1]. The specimens have, however, remained untouched, and Mr. Gardiner has placed them in my hands for description.

The *Laminaria* in question differs from others of the genus in the development of the peculiar bulbous enlargement at the base, from which it derives its name[2]. It further possesses a flat stalk twisted once or twice at the base, while the lamina resembles that of *L. digitata*. The plant has a fairly wide distribution, occurring in Norway, the Faroë Islands, and on our coasts generally. According to Agardh, it extends along the Atlantic shores from Norway to Guinea. It is especially abundant in Cornwall and the Scilly Isles, where it is extensively used for manure. In spite of this abundance, and its marked characters, it was not successfully separated from

[1] In March, 1885, near Penzance. [2] Huds. Flor. Angl., 1778.

[Annals of Botany, Vol. III. No. IX. February 1889.]

other Laminarias by the older writers. Ray, who must have seen it frequently in his journeys, has not separated it from *Fucus digitatus*[1], which is the *Fucus arboreus polyschides* of Kaspar Bauhin[2].

In 1712 Réaumur[3], in a treatise on the 'Flowers and Seeds' of marine plants, describes and accurately figures *Laminaria bulbosa* under the name of *Fucus arboreus polyschides caule plano et tortuoso*, at the same time carefully distinguishing it from Bauhin's and Ray's species. The characteristic flat stalk with the twist at the base, and the hollow bulb with the numerous root-like processes springing from it, are well seen in Reaumur's figure. In spite of this clear separation the species was entirely omitted by Linnaeus.

The name *bulbosa* was applied to the plant by Hudson in the second edition of his British Flora published in 1778. At the time of publication of the first edition in 1762 he does not appear to have met with the plant. According to Esper[4], we must thank Stackhouse[5] and Goodenough, and Woodward[6], for thoroughly describing the plant, and constituting it beyond doubt a distinct species.

Perhaps one reason for this uncertainty regarding a plant with such marked characters is that the Laminarias vary considerably according to locality and other conditions. It is also to be noted that the young *Laminaria bulbosa* has very little resemblance to the mature plant. The stalk is at first cylindrical, and the organs of fixation are similar to those of other species. At an early age there appears a ridge surrounding the stalk just beneath its junction with the lamina. The first notice of this feature I find in Turner's Fuci, 1811, where the young stem is described as 'linear with an umbrella-shaped process.'

Turner states his belief that *F. bifurcatus* of Gunner[7] is really a young stage of *L. bulbosa*; and this he confirms after

[1] Hist. Plant. 1686, p. 75.
[2] Pinax, 364.
[3] Hist. de l'Acad. 1711.
[4] Icon. Fuc. 1797.
[5] Nereis Britannica, 1801.
[6] Trans. Linn. Soc. iii. 153, 1797.
[7] Flora Norwegica, i. 96, 1766.

seeing Gunner's figure. It is fair to suppose that this figure of Gunner's has the umbrella-shaped process described by Turner. I have not been able, however, to obtain a sight of the volumes where *F. bifurcatus* is figured by Gunner[1]; nor have I in any other work met with a figure of a young *L. bulbosa*. Turner further states his belief that Gmelin's *F. bicornis* is identical with *F. bifurcatus*, but I cannot find anything in the description to sanction this assumption. His suggestion that *F. bifidus*, Gm. is also a young specimen of *L. bulbosa* seems to be reasonable. There are no figures of *F. bicornis* and *F. bifidus* in Gmelin's work[2]: but his description of the latter species, founded on a specimen sent by Steller from Kamtschatka, distinctly points to Turner's conclusion. The description of *L. elliptica* by C. A. Agardh, '*radice membranaceo-scutata radiata, stipite compresso in laminam ellipticam integram expanso*[3],' seems again to point to a young stage of *L. bulbosa*. In fact the author himself throws out the query whether this is not the case. J. G. Agardh in his Species Algarum states that he has seen the single specimen on which the species was founded, and quite agrees in considering it as a youthful stage of *L. bulbosa*. He further states that *L. Belvisii*, Ag. does not materially differ from *L. bulbosa*. The specimen of it which he saw was sent from Guinea by Bory to Horneman; and this, perhaps, is his ground for stating that the species extends from the coasts of Norway to those of Guinea —a wider distribution than I have found recorded elsewhere.

Greville[4] mentions that Mrs. Griffiths examined all stages of the plant, and that she bore testimony to its extreme variability according to situation. But Agardh gives the first full and accurate description of the development of the bulb I have met with: 'Below the origin of the lamina there is seen on the stalk a circular line, sharply projecting. This gradually expands into a shield-like lamina whose margin bends downwards all around. It thus becomes hemispherical

[1] Acta Nidrosensia, iv. [2] Historia Fucorum, pp. 192, 201, 1768.
[3] Systema Algarum, 1824, p. 271. [4] Algæ Britannicæ, 1830.

and bell-shaped. The edge of the bell, on touching the rocks, gives rise to root-like processes, which, becoming fixed, render the primary root superfluous. Finally, a hollow bulb is formed sending out processes in all directions[1].' No good series of figures exists of this peculiar morphological structure; and an account of the interesting development of the species is only to be met with by careful examination of books not within easy reach.

The reproductive organs of *L. bulbosa* remained undiscovered for a long time. Tournefort classed all marine plants with those whose seeds and flowers were unknown: but Marsigli appears to have discovered flowers and fruits on several of the Mediterranean seaweeds. The vesicles at the extremities of the leaves of certain Fuci are also mentioned by Ray[2] as containing seeds. Réaumur states that, on a voyage along the coasts of France, he discovered flowers and seeds on several seaweeds, and he published his results in a well-illustrated paper[3]. These flowers and seeds appear to be the conceptacles on the swollen ends of the leaves; but Réaumur does not distinguish the small groups of filaments so frequently met with on all parts of the thallus of many brown seaweeds. So in the following year he published a supplementary paper with the good figure of *L. bulbosa* already referred to, drawing especial attention to the occurrence of these tufts of hairs. 'I have found on many of these plants (i. e. *L. bulbosa*) flowers composed of hairs similar to those which I described for *Fucus major dentata Raii* (evidently *F. serratus*).' He further states that he was unable to find any seeds or capsules.

Later authors seem to have been aware of Réaumur's error, and the fructification is usually omitted in descriptions of the plant. Some, however, have indulged in guesses as to the position of the reproductive organs. Thus Goodenough and Woodward, in their paper in the transactions of the Linnean

[1] Sp. Alg. 1848.

[2] Hist. Plant. p. 1849.

[3] Hist. de l'Acad. 1711, p. 282.

Society, make the following suggestion: 'The apparent bulb is covered with short peziziform excrescences which authors have imagined to be rudiments of other plants. However, as this *Fucus* is always found solitary, we would suggest the idea that they may be receptacles of fructification. We rather dwell upon this idea because in the younger plants there is no appearance of tubercles[1].' This suggestion comes very near to the truth, but it seems to have met with no credence among writers of the time because no grounds of any value were advanced to support it. Turner in 1802 quite ignores the idea, and suggests that the processes from the bulb may be of the nature of the tentacles of *Actinia*, and thus serve to secure the plant to the object of attachment[2]. It is probable, however, that Goodenough referred to the smaller processes on the upper surface of the bulb, while Turner spoke of such as had already become attached to the substratum.

Stackhouse wisely contents himself with drawing attention to the vesicles on the leaves of *L. digitata*, and, from the affinity of this plant to *L. bulbosa*, he expresses 'little doubt that its fructification is in similar vesicles[3].' Such was the state of knowledge when Sowerby in 1807 discovered the fructification of *Alaria esculenta* and *L. bulbosa*: 'On both sides of the furbelows[4], the fructification, hitherto unobserved, is lodged in prominent patches, within whose substance, but quite distinct from the frond, the tubercles of seeds are arranged vertically as in *F. esculentus*[5].' In 1811 Turner described the fructification as 'generally confined to the fimbriated margins of the frond, but sometimes occupying the whole of the stalk or even spreading in broad irregular patches over the lower part of the leaf[6].' Finally, Gardiner in 1885 mentioned the fact that the sporangia are to be found on the swollen root, on its individual processes, and even to the tips of these[7].

[1] Trans. Linn. Soc. vol. iii. p. 183. [2] Brit. Fuci.
[3] Nereis Britannica, 1801. [4] The folded edges of the otherwise flat stalk.
[5] Eng. Bot. No. 1760, 1807. [6] Turn. Hist. Fuc.
[7] Proc. Camb. Phil. Soc. vol. v. p. 224.

External Form.

In the earlier stages of development *L. bulbosa* appears to differ but slightly from other species of the genus. The youngest plant (Fig. 1) with which I am provided consists of three parts—an oval expanded portion, the lamina, two inches long and one inch broad; a short cylindrical stalk; and this passes downwards into several rounded expansions which serve for the attachment of the young plant. At a short distance below the junction of the lamina and the stalk there is already developed the ridge which represents the commencement of the bulb. There is in this specimen a curious prothallus-like expansion attached to the stalk. This appears to be one of the attaching processes which, instead of becoming applied to the substratum, has grown up and almost fused with the stalk.

The early development of many Algae has been patiently worked out by Strömfelt[1]. Unfortunately his short paper on the subject is without figures, and professes to be of the nature of a prefatory notice. Until the larger work with figures appears we must be content with such brief descriptions as he gives. Strömfelt divides the embryonic organs of fixation of Algae into three classes, according as they develope on germination,—1. a primary root-cell; 2. a creeping branched cell-row; 3. a cushion-like cellular mass. After describing various lower Algae as falling under the second division he states that probably all the (Norwegian?) Phaeozoosporeae belong to the same type. Of *Laminaria* he writes thus: '*Laminaria* shows in many points a close relation to the Phaeozoosporeae, and probably agrees with them in that it is developed from a simple cell-row; but the organ of fixation undergoes so many changes during development that it deserves a separate notice. At first root-threads are developed, as for example in *Chorda* or *Ilea*, but here they remain unicellular and free. The basal portion of the shoot becomes rounded to form the stalk, and the lower part of this forms a thick basal bulb as a

[1] Bot. Centralblatt, xxxiii.

consequence of energetic cell-formation. This bulb increases rapidly in diameter and grows downwards, pressing closely on the substratum. It thus surrounds the root-threads which spring from the middle of its lowest part, and causes their destruction. At this stage of development the sole means by which the plant is fixed is the basal bulb. It may be that the root-organ of *L. solidungula* has remained stationary at this stage of development. In our common species there are developed from the upper part of the bulb and neighbouring parts of the stalk several successive whorls of root-branches. The median strand of elongated cells which is found in the stalk is wanting in these organs. The root-branches grow towards the substratum and become applied to it with great force: so much so, that in older specimens the original fixing bulb is loosened from its attachment and lifted away. This is certainly the case with *L. hyperborea* which possesses a stronger and more regularly developed organ of fixation than the other species. *Alaria* has a similar organ, but frequently less strongly developed[1].' As no special mention of *L. bulbosa* is contained in the passage just quoted, I presume that Strömfelt has not met with it in the earlier stages, for such a deviation from type would not be omitted even in a prefatory notice.

After a very moderate development of processes from the basal part of the stalk, further outgrowths from this part of the plant appear to cease. All further development of fixing organs is now confined to the ridge of tissue already referred to. The portion of the stalk below the ridge does, however, for a certain time grow in length and thickness, and continues to be the longest part of the stalk.

The development of the ridge, and its gradual transformation into a bell-shaped organ, are represented in the series of figures accompanying this paper. These figures may be briefly interpreted by referring to Agardh's short description already quoted. In Fig. 2 the stalk is already assuming its flattened form. This is emphasized in Fig. 3, where also the ridge is

[1] Bot. Centralblatt, xxxiii. p. 398.

beginning to curve downwards. There is a great gap in the series between this specimen and the next. A gradual downward growth of the umbrella-shaped appendage must be assumed, accompanied by a formation of finger-like processes at its edge. There is at the same time a considerable increase in size of all the parts, and there appears also the twist in the stalk which is characteristic of the species. In the further description of the finger-shaped processes I shall make use of the term '*hapteres*' introduced by Warming[1] for the peculiar organs of attachment among the Podostemaceae, and applied by Wille[2] and others to the fixing organs of *Laminaria*. The primary organ of fixation is not so easily included under the term, because it is part of the main stem and not an outgrowth from it. It differs furthermore from the hapteres in its anatomical structure, possessing as it does a central strand of elongated cells.

In Fig. 4 the primary organ of fixation is seen from below inside the bell: there is only one circle of hapteres developed. Fig. 5 represents a stage at which three such circles are being formed. The oldest are already fixed; the part of the bell above these has expanded considerably by intercalary growth, and the second row of hapteres now occupies the position formerly taken up by the first row. The third row is just appearing above the second. It will readily be seen from the figures that on attachment the distal ends of the hapteres become disc-shaped.

In Fig. 6 this mode of growth has proceeded further. Here the excessive growth of the upper part of the bell has resulted in the formation of a flat hollow bulb. Four successive circles of hapteres have made their appearance, three of which are represented in the ground-plan (Fig. 7), while the fourth is not visible from the under-surface of the bulb. The degree of

[1] Bot. Zeit., Notizen, No. 12, 1883. 'These hapteres arise exogenetically, and their branches are exogenous. They grow principally at the apex, and have a naked end (i. e. covered by no root-cap). They are formed of parenchyma alone, without trace of vascular bundle.'

[2] Bot. Centralblatt, xxvii, 1–6.

attachment corresponds fairly well with the irregularity of outline of the disc-end of the haptere. The primary organ of fixation, *f*, has fused with hapteres of the first row. It has not yet been torn away from its attachment by the formation of the wide base of the bulb. It will be seen at a glance how great an increase in stability is attained by such an extension of fixing base. Only some of the second row have reached the substratum, while those of the third row are still comparatively small.

Fig. 8 shows a double twist at the base of the stalk: the flat portion above the twist shows a perfectly straight outline. The lamina is splitting up into its numerous segments, and the bulb has assumed an irregular form. Finally, Fig. 9 represents a specimen which is a good deal older than any yet figured. The great hollow bulb has been formed, and has assumed the dark opaque colour of the adult. The numerous tubercles may or may not represent series of rudimentary hapteres, although, under normal conditions, it is improbable that any of them would develope into attaching organs. The further development includes further changes. The bulb may reach a much greater size. The specimen figured by Stackhouse[1], at natural size, measures 10½ inches across; and it is stated that a specimen has been collected which measured a foot in diameter. In spite of this great increase in size, the bulb remains hollow, and its walls do not increase in thickness to any appreciable degree.

Fig. 10 represents a portion of an old bulb on which sporangia are plentifully developed. These are present on all parts of the outside of the bulb, as well on the surface of the bulb itself as on the tubercles developed upon it; and the sporangia cover these tubercles to their tips. They are not, however, confined to the external surface, but are also plentifully developed on the inner surface of the hollow bulb.

The stalk soon becomes differentiated into two parts by the development of the ridge. The lower part remains

[1] Nereis Britannica, 1801.

cylindrical, and does not greatly increase in thickness. For a considerable time, however, it is the longer part of the stipes, and not until the bulb has become well attached does it lose its importance as the principal fixing organ. The portion above the ridge commences very early to assume a different form to the lower portion. At a time when the ridge itself is hardly perceptible the cells of the upper part show a marked difference from those of the lower. The central cells have assumed an irregular course, and very quickly exhibit the winding, twisted appearance of the so-called 'hyphal tissue.' At the same time the transverse section here becomes oval, and the median strand of hyphal tissue appears as a line along the greater diameter. The stalk then becomes flat and twisted, but remains short (Figs. 3, 4). It is not until the bulb is well developed that the elongation of the stipes is marked, growth taking place at the point of junction of the stalk and lamina. A straight, ribbon-shaped piece arises by intercalary growth between the twisted portion and the lamina (Fig. 8). The greatest length that the stalk appears to attain is somewhat over two feet, but its length depends on the depth of water in which the plant grows[1]. Two or three stalks may arise from one bulb.

This appears to be a not uncommon phenomenon among the Laminarias. Le Jolis[2] saw several specimens of *L. hyperborea* divided dichotomously to the middle or base of the stalk; and in Lenormand's Herbarium he observed a specimen of *L. digitata* bifurcated. Turner[3] has cited a case of *L. digitata* forked at the summit, each half bearing a lamina: and De la Pylaie[4] mentions a similar case. Agardh[5] thinks that the branching is due to a split of the lamina being produced downwards into the stalk; but Le Jolis regards this as impossible, for, in the *L. hyperborea* examined by him in the living state, there were no signs of tearing. From the cases mentioned it appears that the branching of *L. bulbosa* is due either to a split of the lamina extending down the stalk, or to a real bifurcation of the plant. The healing of a split is very readily traced on making a section. It would therefore seem probable that the explanation of Le Jolis is the right one. And in this case the branching must occur at a very early period owing to the peculiar intercalary growth of all these plants. There is, however, a third method by which such

[1] Greville, Algae Britannicae, 1830.
[2] Nov. Act. Acad. Leop. Car. xxv. 1855.
[3] Hist. Fuc. t. iii. p. 68.
[4] Flore de Terre Neuve, p. 24.
[5] Sp. Alg. i. 135.

a branching could be brought about, and that is by the fusion of several plants which have germinated side by side. Reinke, in his paper on *Fucus vesiculosus* [1], suggests this explanation for those cases where several plants of about equal size spring from the middle of one disc of attachment. The tissues of these Algae would certainly lend themselves to such a fusion, because of their exceedingly well marked 'gliding growth.' In support of his suggestion Reinke refers to a figure of Kützing's [2], where an individual of *Fucus vesiculosus* and one of *F. serratus* spring from the same disc. If this is the case with the several-stalked *Laminaria bulbosa*, the fusion must have taken place in the young plant as far as the point where the ridge would arise.

The lower part of the flat portion just above the twist soon becomes altered. The edges appear to grow in length far more rapidly than the median part. The result is that they are very much convoluted, while the median portion is perfectly flat. This is well seen in Fig. 23, which is copied from that given in Harvey's Phycologia Britannica. The curious foldings of the stalk have long been noticeable enough to earn for the plant the popular name of 'Sea furbelows.' It was on these furbelows that Sowerby first detected the sporangia.

Thus the stalk during development becomes differentiated into the following parts. 1. The primary fixing organ below the ridge. 2. The ridge itself with the organ developed from it. 3. The flat, twisted portion immediately above the ridge. 4. The part with convoluted edges. 5. The upper flat portion, which passes somewhat suddenly into the widely expanded, much divided frond.

To describe the shape of the lamina in detail does not come within the scope of this paper; and, even if suitable material were procurable, such a description would not be of much value; for the lamina varies greatly, and, according to Agardh, 'from the form of the frond no distinct characters are to be obtained [3].' The lamina is at first entire (Fig. 1), and contains many small pits with filaments protruding. These are the 'flowers' of Réaumur; and the filaments, according to Greville, are merely the free ends of the cell-rows at the mouth of the pit. The subsequent

[1] Pringsh. Jahrb. x. p. 318. [2] Phycol. general. x. t. 11.
[3] Sp. Alg. i. 134.

development appears to be simple enough. The oval lamina becomes early split up (Fig. 3), and the wounds caused by the splitting are healed by the formation of a new epidermis over the exposed part.

The lamina grows to a very large size, and in the mature plant consists of very many narrow-pointed segments. The plant is easily recognised as the largest European seaweed, and one whole plant is stated to be a sufficient load for a man to carry on his shoulders. The parts of the lamina, when spread, may measure from six to twelve feet across.

Arrangement of Tissues.

The increase in thickness of *L. bulbosa* appears closely to resemble that described for *Durvillaea Harveyi* by Grabendörfer[1]. This member of the Fucaceae also approaches the Laminarias in the absence of the vegetative cell at its apex. The peripheral cells give rise to new cortical cells by the formation of tangential walls, thus having the character of a meristem rather than that of a true epidermis. It will, however, be found convenient to retain the term epidermis in the following descriptions.

A similar increase in thickness seems to be present in other Laminarias, but in *L. bulbosa* the epidermal region appears to be the only one in which active cell-division can be observed to take place. One would naturally expect that, in the excessive development of one part of the stem attendant on the formation of the ridge, there would be indications of a rapid cell-formation occurring in the peripheral meristematic layer. Such, however, does not appear to be the case ; all that is seen in section is a hemispherical expansion of the stem, and the outgrowth at this point seems to be due to the rapid increase in size of the cortical cells. In a section through this, or any other, part of the plant (Fig. 11), the epidermal cells are small and cubical,

[1] Bot. Zeit. 1885.

with a thicker outside wall resembling a cuticle. The cells are densely filled with chromatophores, and usually appear to contain one nucleus; not unfrequently they are seen to be divided by thin tangential and radial walls. Further, the cells immediately beneath the epidermis are often evidently derived from this layer by a similar division of cells. But the cells of the third layer from the exterior have usually so grown in size and altered their shape that it is difficult in many cases to trace their origin. This fact seems to indicate that the growth of this Laminaria by the formation of new cells is exceedingly slow. Whether this be so or not there are no indications of the presence of any other meristematic zone in any specimen I have examined, such as that readily observable in a transverse section through the stalk of *Alaria*.

In passing toward the centre of the stem the cells increase in size, retaining their general rectangular form. Such cells form the cortex, and are more or less sharply marked off from the central strand of tissue, which has been termed the medulla. In the latter layer the cells become elongated, usually in the direction of the long axis of the part; and they frequently assume an undulating course. Fig. 12 represents a portion of the medulla taken from the stalk of a young specimen just above the ridge. It will be seen that the undulating course is accompanied by a great increase in the thickness of the longitudinal walls of the cells. The section would show a number of tubes running side by side through a clear matrix. The pits connecting neighbouring tubes assume the form of short tunnels, and very early the cells send out processes into the thickened walls. These become hypha-like outgrowths, and penetrate the substance of the walls in all directions; they become divided by transverse walls and form a felted network, which, in transverse section, may assume the appearance of parenchymatous tissue. The formation of this hyphal tissue is another item in the growth in thickness of the plant, and is also met with in many other seaweeds. It is interesting to note

that in those parts which do not increase in thickness, viz. the stipes below the ridge and the hapteres, there is no formation of the hyphal tissue. Figs. 13 and 14 represent the hyphal tissue of the lamina. There appears to be another form in which this budding of cells occurs. In a longitudinal section through an older part of the stipes a central strand of small elongated cells and tubes is met with. The cells between this strand and the cortex are elongated and large; they appear to be separated by intercellular spaces (Fig. 15), and the latter are in some cases crowded by small, rounded cells. The larger cells appear to be separated by rows of smaller ones; but the rounded contour of the latter, their frequent wide separation, and their irregularity, show that they do not form a tissue. They remind one, indeed, at first glance, very forcibly of thyloses. The large cells have many pits upon their walls, and the formation of a protrusion appears to take place over or at one of these pits.

The epidermal cells usually contain only one nucleus. This is not the case with the other cells of the plant. A rapid increase of nuclei seems to be the normal course of events, and in some of the older cells thirty or forty may readily be counted, sometimes arranged in rows to the number of fifteen or sixteen (Fig. 16). In some cells each nucleus is surrounded by a group of chromatophores (Fig. 17).

It appears to me that there is some misconception as to the number of nuclei present in the cells of brown seaweeds. Zimmermann, in his work on 'The Morphology and Physiology of the Plant Cell,' dismisses the group with the following statement:—'Among the Phaeophyceae Schmitz always found only one nucleus in each cell: only in the hair-cells of the conceptacles of *Cystoseira barbata* did he observe frequently several nuclei[1].' This would seem to imply that Schmitz had made a study of the group. But Schmitz's words show that he examined only a few forms; and these were mostly simple ones. He writes: 'Among Phaeophyceae I have also found the vegetative cells to be always uninucleate *in the species of Cladostephus, Halopteris, Sphacelaria, Ectocarpus, and Discosporangium which I examined.* The same holds good for *Aglaozonia reptans*, Cr. Multiplication of nuclei in single cells is not, however, entirely wanting among the brown Algae, as is proved by an observation on *Cystoseira barbata*[2].' . . . . There does not

[1] Schenk's Handbuch, iii. 2, p. 518, 1887.
[2] Verh. d. naturh. Ver. Bonn, 1880, p. 128.

appear to be any mention of nuclei in the works of Reinke, Dodel-Port, Wille, Will, Humphrey, and Grabendörfer; and the exquisite drawings of Riocreux in Thuret's Notes Algologiques are unfortunately not distinct on the point. I have no doubt that in the Phaeophyceae, as in the Rhodophyceae, the greatest variation in this respect occurs. In the latter division of Algae the greatest diversity prevails. Thus, according to Schmitz, of different species of *Callithamnion*, some have only uninucleate cells (*C. plumula*, etc.); in others the young cells have single nuclei, but when they increase in size the cells have several nuclei (*C. granulatum*, etc.); finally, in other species, the youngest cells of the growing apex have several nuclei (*C. Borreri*, etc.) [1]. The number of nuclei present in the cells of these plants seems then to be of no systematic value; there is, however, such a marked uniformity in some groups (Siphoneae) that the character may become of importance in this respect. I regard it as very probable that multinucleate cells will be found in many of the larger brown seaweeds; and they might be especially sought for in the cells of the hyphal tissue.

It has been stated that at the formation of the ridge there is no appearance of special activity in the epidermal cell-division at this point. At the very earliest indication of a swelling round the stalk there is, however, a marked change in the arrangement of the cells of the pith and cortex. The cells of these parts, and especially such as form the boundary line between them, become much larger than the rest. The elongation takes place in a direction curving obliquely outwards towards the epidermis; and the appearance suggests that these cells become elongated and push the external cells outward before them. Here, as in other parts, the increase in thickness of the stalk is due rather to the growth of the cells than to their increase in number. There is, accompanying this enlargement of the cells, a great development of their walls, and an early formation of the hyphal tissue; so that in this respect, also, the manner of growth appears to be the same at the ridge as it is in other parts.

As already mentioned, the growth above differs from that below the ridge. It is not easy to compare the thickness of these parts at different ages, because the part of the stalk above the ridge immediately assumes a flattened form (Fig. 2), while the primary fixing portion retains its circular, transverse section. There appears to be an entire absence of the hyphal

[1] Verh. d. naturh. Ver. Bonn, 1880, p. 125.

tissue below the ridge, although the cells of the central strand retain their elongated character (Figs. 18 and 19).

The absence of the hyphal tissue below the ridge leads one to interesting speculations as to the use of this layer to the organism. The position of this tissue and the elongated character of its cells immediately suggest that it is of use in transport. As such it is regarded by those who have made a special study of the larger seaweeds (N. Wille)[1]. This idea is strengthened by the discovery of the perforated transverse plates by Wille and Will, as also by the close connection of the hyphal tissue with the sieve-tubes of *Macrocystis* (H. Will[2]) and of *Nereocystis* (Oliver[3]).

The formation of the ridge seems to be very closely connected with the formation of the hyphal tissue. The great increase in size of the cells of this neighbourhood renders it necessary that large stores of material shall be hurried down the narrow stalk from the centre of assimilative activity. Such a need leads to the great increase of the path of transport at this point, and hence the almost immediate assumption of the oval form of the transverse section of the stem. As the ridge developes, a core of hyphal tissue accompanies it, thus rendering possible the great development not only of the bulb itself but of the numerous hapteres, and, in the older plants, the masses of sporangia.

The development of the hapteres commences like that of the ridge. There is, however, no bending out of cells, nor any formation of hyphal tissue. The transverse section of one of the hapteres (Fig. 20) reminds one forcibly of that of a phanerogamic water-plant. There is a moderately developed cortex of smaller cells passing into the usual epidermal meristematic layer. The central larger part of the section is occupied by cells of two kinds—larger cells distributed at equal distances, and rows of smaller cells surrounding and separating them. The large cells call to mind the intercellular spaces of water-plants, but they are cells with protoplasmic lining, and many nuclei. In

[1] Berichte d. deutsch. bot. Gesellsch. 1885, p. 29. [2] Bot. Zeit., 1884.
[3] Annals of Bot., vol. i. (1887), p. 95.

one of the older hapteres they are filled with dense brown contents. In a longitudinal section they are seen to be of great size, and the whole haptere appears to be of a spongy consistence. There is no strand of tissue in the haptere at all comparable with the narrow elongated elements representing the transport tissue of other parts; and in this respect the resemblance to the true hapteres of Podostemaceae, described by Warming, is very striking. In both cases we have merely to do with the primary fixing function of roots, the secondary function of absorption does not come into play.

The increase in size of the haptere seems to be due in very great measure to the distension of its cells. The epidermis remains comparatively inactive as long as the substratum is not reached. As soon, however, as the haptere touches the substratum, as for instance a piece of rock, the epidermal cells appear in a new light. Each cell grows out after the manner of a root-hair, often apparently while at some distance from the piece of rock: a cubical basal portion is cut off, and usually several transverse walls appear in its course (Fig. 21). The ends of these rhizoids become attached after the manner of root-hairs of Phanerogams to any particles on the surface of the rock. It is probable that such intimate contact is not accompanied by the solution of the particles, but merely contributes to the firmness with which the plant adheres to the substratum.

This activity of the epidermal cells on approaching the substratum is very unlike the condition described by Grabendörfer[1] for the fixing organs of *Durvillaea* and *Lessonia*. In *Lessonia ovata* the capacity for division leaves the epidermal cells the moment they touch the substratum; and in *Durvillaea* they quickly become permanent and filled with dark contents. Those epidermal cells which are nearest the latter, but which are still free, undergo division, and are pressed in turn against the substratum by the increase in size of the part; and thus a continually increasing surface is formed which, by pressing into all the unevennesses of the rock, forms a firm attachment for the plant. This formation of root-hairs is not confined to *L. bulbosa*. Thus, numerous root-hairs are formed on the hapteres of *Pycnophycus*. In *Alaria esculenta*, on the under side of the rhizome-branches, the epidermal cells grow out in bunches or masses to unicellular root-hairs[2]. There are in this species, according to Reinke, bunches of outgrowing epidermal cells on the lamina as well. These hairs, however, whose

[1] Reinke, in Pringsh. Jahrb. x (1876).

function is absorptive, represent the bunches of filaments projecting from the pits of other species.

The development of the sporangia appears to take place in exactly the same manner as that of the rhizoids (Fig. 22). Epidermal cells become elongated, and a basal part is cut off from each: the distal end becomes either one of the paraphyses or a unilocular sporangium. This occurs all over the bulb on the inside as well as the outside.

Differences from other Laminarias.

The differences between *Laminaria bulbosa* and allied species are seen as well in the formation of the bulb and stalk as in the position of the sporangia. As has been already mentioned, *L. bulbosa* was not separated from *L. digitata* for a long time—this being probably due to the similar character of the thick lamina. There are, as will be seen, numerous peculiarities in *L. bulbosa* marking it off very sharply from every other plant.

Foslie, in a paper on the Laminarias of Norway[1], divides them into three classes according to the development of the hapteres. *L. bulbosa* is not included in the list, presumably because it is to be placed in a separate genus. In the first type, *L. hyperborea* (=*L. Cloustoni* of text-books, Cuvy of Clouston), 'the hapteres are strong; they are arranged in regular or nearly regular vertical series, and the primary haustorium is early loosened from the substratum.' *L. digitata* (=*L. flexicaulis* of Le Jolis, Tangle of Clouston) is put forward as a second type with 'hapteres in more or less horizontal, less regularly alternating whorls: the haustorium frequently retains its position till the end of the plant's life.' The third type includes those in which the 'hapteres are usually thin, much branched, long and pointed, almost always irregular in distribution.'

In all other Laminarias then, the hapteres arise as emergences,

[1] Ref. in Bot. Centralblatt, xxii. 193.

and appear in ascending order in more or less regular series—in this respect resembling the adventitious roots of such a plant as *Zea Maïs;* but in *L. bulbosa* the development of hapteres is restricted to one part of the stalk, and in fact to the bell developed below its junction with the lamina. This organ is not, however, to be regarded as the fused bases of many hapteres, for it is a process of the stalk and differs markedly in histological characters from the hapteres.

In this respect *L. bulbosa* differs very greatly from the other Laminarias; and since the development of the hapteres is the character on which specific differences are based, there is perhaps a sufficient gap between our species and the rest to constitute it a separate genus. In looking through the synonyms of *L. bulbosa* one meets in fact with no less than three generic names. Decaisne seems to be responsible for two of these—*Haligenia* and *Saccorhiza*, the latter being founded on De la Pylaie's suggestion. Kützing is responsible for *Phycocastanum.* Unfortunately I have not had access to the descriptions of these authors. Agardh[1] has accepted De la Pylaie's genus *Saccorhiza*, and finds the differences mainly in the character of the 'root': the development of the sporangia upon the furbelows is also mentioned as a generic character.

In other Laminarias the sporangia are confined to blisters on the flat lamina. In *L. bulbosa* they are developed on the bulb, on the furbelows and other parts of the stalk, and on the basal parts of the lamina. Differences in the position of reproductive organs are usually regarded as of great importance in distinguishing plants, and great stress was laid by the earlier writers on the presence of the sporangia on the furbelows. In the position of the normally placed sporangia this plant resembles *Alaria esculenta.* In the latter, special outgrowths from the stem, bearing the reproductive organs, appear at about the same point beneath the base of the lamina, as the ridge in *L. bulbosa.* These outgrowths are arranged in two rows, and appear in the same plane as the two wings of the

[1] Sp. Gen. et Ord. Alg. 1848.

lamina. The upper ones, by their flattened character, evidently represent feebly developed leaves; they are not, however, derived from the main lamina by splitting, but arise independently as emergences from the stalk[1].

The species *L. digitata* and *L. hyperborea*, included in the subdivision Digitatae, resemble *L. bulbosa* in the tough and leathery character of their laminas. There is, however, a peculiarity in these species which I have not found attributed to *L. bulbosa*. This consists in the well-known annual shedding of the lamina, and the development of a new one by intercalary growth at the point of junction of stalk and lamina. A similar phenomenon is also a marked character in *L. saccharina*, and is stated by Reinke to occur in *Alaria esculenta*[2]. It has been maintained that this shedding of the lamina is present in *L. hyperborea*, but is not shared in by *L. digitata* (Le Jolis, Clouston); but Foslie states that the observations on which this conclusion was based 'rest on a wrong interpretation of the facts.'

The stalk in those Laminarias which are at all closely allied to *L. bulbosa* is cylindrical: it is not divided into regions, and the development of the ridge and its hapteres is entirely wanting.

Concluding Remarks.

It remains to summarise and discuss such results as have been given; although on account of the short time the specimens have been in my hands, and the lack of old material, I have been unable to investigate many points in such a manner as they seem to merit. The main object of this paper is the description of the development of the bulb and its illustration by suitable figures. The general course of development, as also the peculiarities of the stalk in this *Laminaria*, may be readily learnt by reference to figures 1 to 10 and 23. It is very evident to any one who studies the literature of the subject that this *Laminaria* has been com-

[1] Agardh, in Bot. Zeit., 1874, No. 35.
[2] Pringsh. Jahrb. x. 1876.

paratively ignored. And yet the plant was well described at the beginning of last century, and the development of its bulb appears to have been known at the commencement of the present century. The first, and in some respects, best description is that of Réaumur in 1712. The most useful general account appears in Turner's works, 1802–11: while the most accurate description of the development of the bulb was given by Agardh in 1848. The position of the sporangia, long unknown, was first discovered by Sowerby on the furbelows in 1807: while not until 1885 was their presence on the bulb demonstrated.

In the stalk there are five regions: 1. The primary fixing organ; 2. the bulb; 3. a flattened twisted portion; 4. a portion with flounced edges; 5. a flat straight piece which passes upwards into the lamina.

It is difficult to make dogmatic statements as to the absolute significance of these parts. There can, however, be little doubt that the bulb has principally to do with fixing the plant to the sea-bottom. Its great increase in size and the development of successive circles of hapteres can only point to this conclusion. It is of further use, however, in forming a lodgment for sporangia: and probably, where not forming sporangia, the epidermal cells assimilate. So that if all the rest of the plant be torn away, as frequently happens in storms, there is still left in the bulb the possibility of assimilation and reproduction. The twisting of the stalk above the bulb causes it at this point to approach the form of a hollow cylinder—an arrangement obviously conferring a great increase of rigidity on this part. The greatly expanded part with convoluted edges, above the twist, appears to have a twofold function: firstly, it bears sporangia, and secondly, the arrangement of the edges in folds must add strength and rigidity.

A similar explanation is given of the foldings in the stem of *Caulotretus heterophyllus* described by Warburg; but in the latter case the median part is convoluted and the edges are perfectly flat. *Caulotretus* is a liana allied to *Bauhinia*; and Haberlandt suggests the very natural explanation that the plant, by this peculiarity of the stem, acquires sufficient rigidity to enable it to reach branches to which it may become attached[1].

[1] Physiolog. Pflanzenanatomie, p. 383.

There appears then to be a distinct aim at rendering the flat stalk as rigid as possible, and thus more securely to bear the huge frond attached to it. Finally, the flattened upper part of the stalk just below the lamina is more readily bent than other parts, and may act as a hinge.

It will be seen from the figures that, in the early stages, the stalk of *L. bulbosa* is cylindrical; and this may be regarded as evidence of the descent of the species from a form more nearly resembling those other Laminarias, in which the stalk is still rounded. There is a great amount of morphological differentiation in this species, and it appears to represent a specialized type when compared with the other members of the genus. It is not easy, however, to assign a reason for the departure of the stalk from its rounded form. Greater strength might be aimed at; but any amount of strength may be obtained by the secondary thickening found in round-stalked Laminarias. A tendency towards the increase of the assimilating surface, so apparent in the huge development of the lamina, may have extended its influence to the stalk as well. Or, lastly, the tendency of the sporangia towards the 'roots,' in this species as in *Alaria*, might be facilitated by a flattened and subsequently folded stalk.

There seems in this plant, as in *Alaria*, to be incipient separation of the assimilating and reproductive regions which are still united in other Laminarias. It is interesting to contrast these plants with those growing on land. In the latter the spores are usually non-motile, and are dependent on various external influences for their dissemination. Their reproductive organs are therefore situated in the most exposed situations at the summit of the stalk or at the end of a branch. Here, however, the spores are motile, and everywhere around them is the medium in which they may disperse themselves; accordingly it is rather of advantage than otherwise that the sporangia are developed nearer the base of the plant. The sporangia are thus more sure of being undisturbed, and the spores are nearer to the substrata, to which the young plants become fixed.

Although we cannot state that the flattened form of the stalk is due to the necessity of supporting the huge leaf, we may yet safely conclude that the various other attempts at rigidity, and secure foothold, were caused by the great development of the lamina. An enormous assimilating surface has been formed, and it must be supported. The plant appears to

have over-exerted itself in this respect, and in spite of all its attempts does not escape being torn up bodily and cast on the shore.

The facts just mentioned seem to indicate that *L. bulbosa* is an advanced type with a great amount of differentiation, and complicated attempts at adaptation. There does not seem to be a corresponding amount of histological differentiation. In fact, in this respect, it appears to possess a much simpler structure than allied species. Unfortunately I have not succeeded in examining older specimens, and the appearance of complexity in the tissue frequently takes place comparatively late in other Laminarias. In the first place, I have not met with any zones of secondary thickening. This occurs in the stalks of other Laminarias and may be absent in *L. bulbosa* because of the flatness of this organ. At the same time the hapteres of *L. saccharina* and *L. digitata* increase in thickness in this manner, and I find nothing of the kind in the hapteres of *L. bulbosa*. Then, again, I have not met with any appearance of the mucilage-ducts found in various other Laminarias; and the development of the trumpet-hyphae does not appear to be at all well marked. Finally, the presence of huge cells with many nuclei is certainly characteristic of the species, since this is largely prevented in other Laminarias by the appearance of zones of secondary meristem. This character, and the consequent increase in size of many parts by the increase in size of individual cells, rather than the multiplication of cells, seem to point to a low stage of histological differentiation.

I have to record my thanks to Mr. Walter Gardiner for the material which I have examined, and for his assistance in arranging the subject-matter of this paper, and also for many valuable suggestions during its preparation.

Botanical Laboratory, Cambridge,
September 1888.

DESCRIPTION OF FIGURES IN PLATES V AND VI

Illustrating Mr. Barber's paper on the Development of the Bulb in *Laminaria bulbosa*.

Figs. 1, 2, and 3. Young plants of *L. bulbosa*, showing the origin of the ridge from which the bulb is developed. Natural size.

Fig. 4. Lower part of older plant, with bell-shaped organ of fixation developed from the ridge: the primary fixing organ is visible in the centre of the bell. Natural size.

Fig. 5. Vertical section through bulb of an older specimen, showing the development of three successive circles of hapteres. Natural size.

Fig. 6. A somewhat older bulb with numerous hapteres. Slightly reduced.

Fig. 7. Ground-plan of the same viewed from below, showing the circles of hapteres developing in a centrifugal manner. The primary organ of fixation, *f*, is seen at the centre, and has fused with the innermost hapteres.

Fig. 8. Plant of *L. bulbosa* about two feet long. The furbelows are not yet developed.

Fig. 9. Older bulb, from which the stalk and lamina have been torn. × $^2/_3$.

Fig. 10. Part of an old bulb covered with tubercles. The whole is brown with sporangia.

Fig. 11. Section through epidermis and cortex of stalk at ridge (same specimen as in Fig. 19).

Fig. 12. A portion of the medulla of the stalk above the ridge (of the same specimen), in longitudinal section. The walls of the cells have become thickened, and hypha-like protrusions are being sent into the thickness of the walls.

Fig. 13. Portion of the medulla in the transverse section of the lamina (specimen in Fig. 8).

Fig. 14. The formation of a hyphal protrusion from a single cell of the same.

Fig. 15. Longitudinal section through stalk of same specimen. Some of the cortical cells near the medulla are figured: only a part of the two large tubes is shown.

Fig. 16. Hyphal cell with many nuclei; obtained from specimen in Fig. 3 in a transverse section through the stalk at the ridge. This section is stained with haematoxylin, and was cut, like most of the others, in paraffin by the microtome. The hyphal cell passes out at right angles to the stalk into the developing ridge.

Fig. 17. Cell with many nuclei and chromatophores; one of the large cells in the cortex of Fig. 19.

Fig. 18. Cells of medulla below the ridge; from a very young specimen (Fig. 1).

Fig. 19. Longitudinal section through a stalk at the ridge; from a slightly older specimen.

Fig. 20. Cells from the transverse section of a haptere; the haptere was taken from specimen in Fig. 6.

Fig. 21. Longitudinal section through the apex of an attached haptere with rhizoids: the haptere was taken from the same plant.

Fig. 22. Section through epidermis of bulb represented in Fig. 10, showing sporangia and paraphyses. The sporangia are unilocular.

Fig. 23. Copied roughly from figure of Harvey's in Mrs. Gatty's British Seaweeds. Supposed to represent an old plant of *L. bulbosa*.

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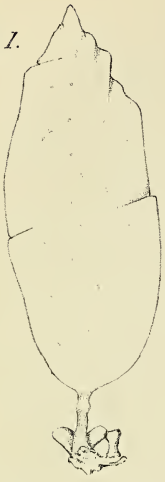

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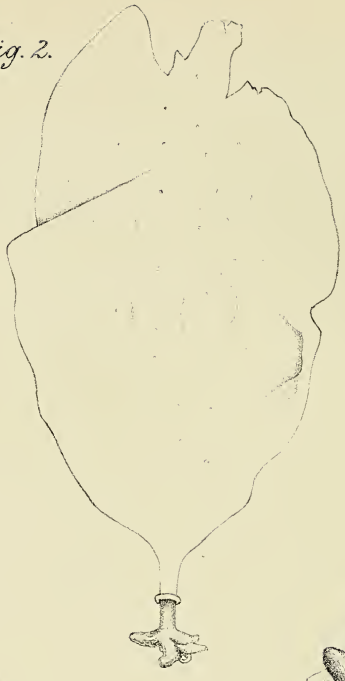

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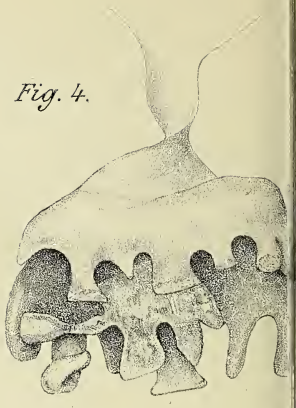

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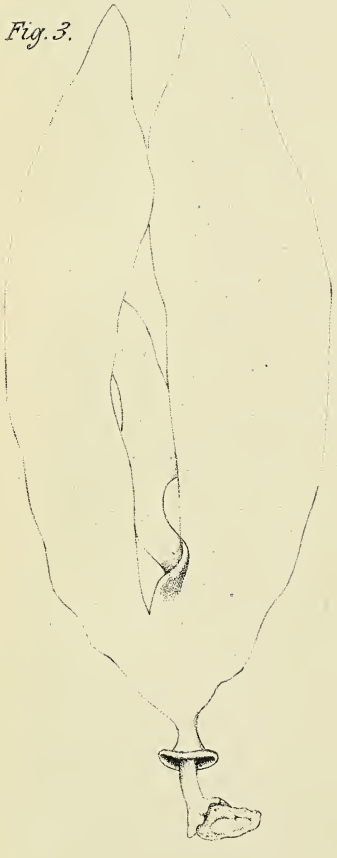

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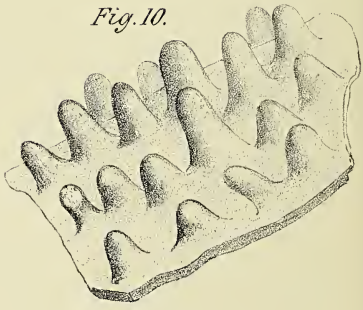

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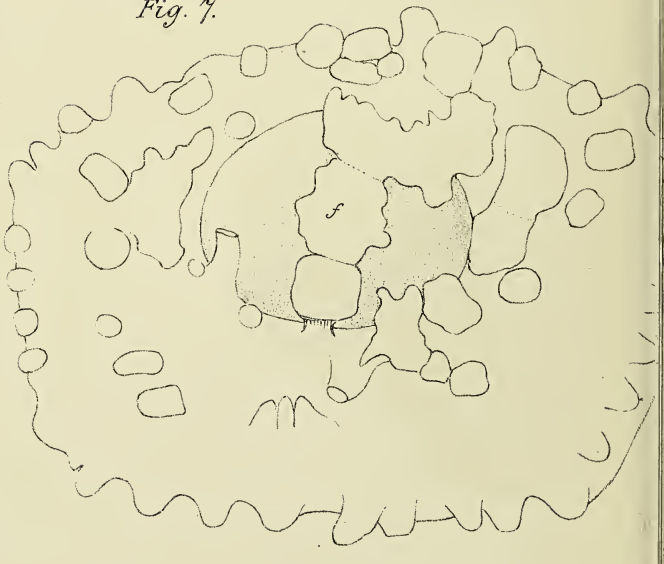

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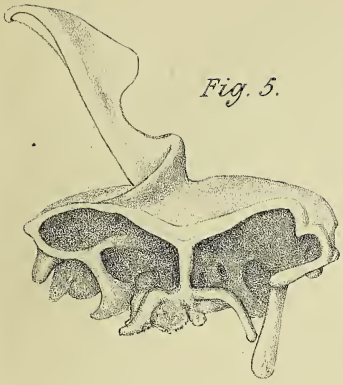
Fig. 5.



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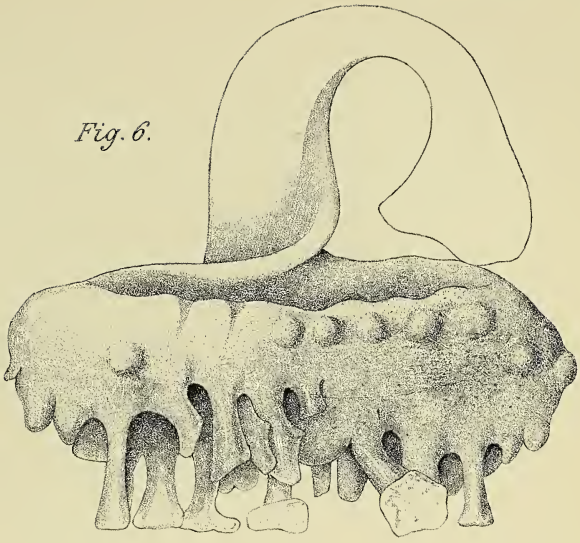

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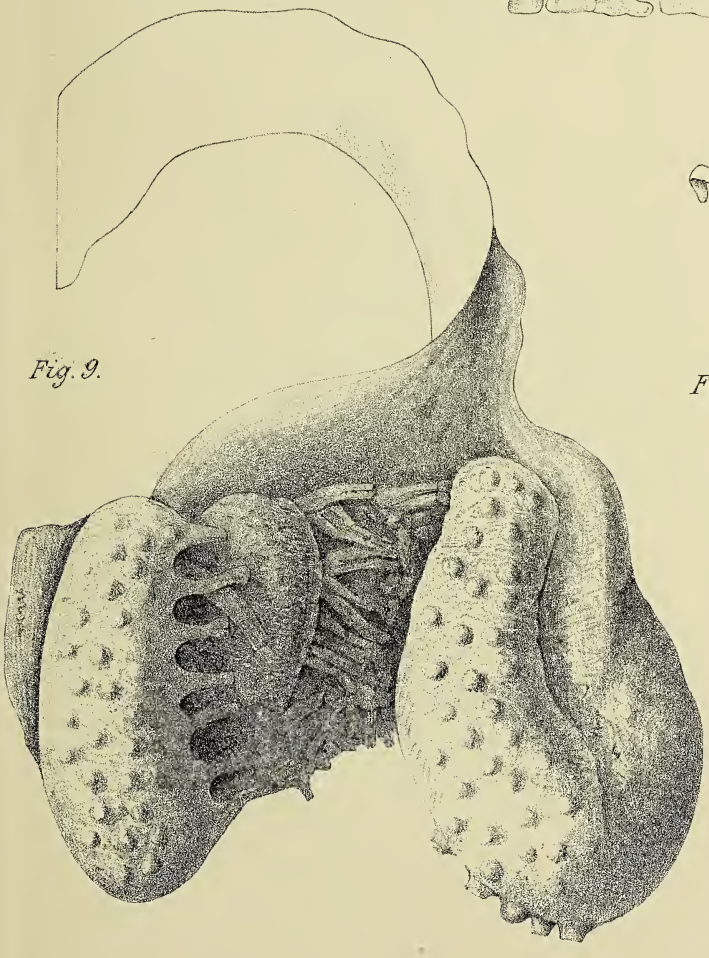

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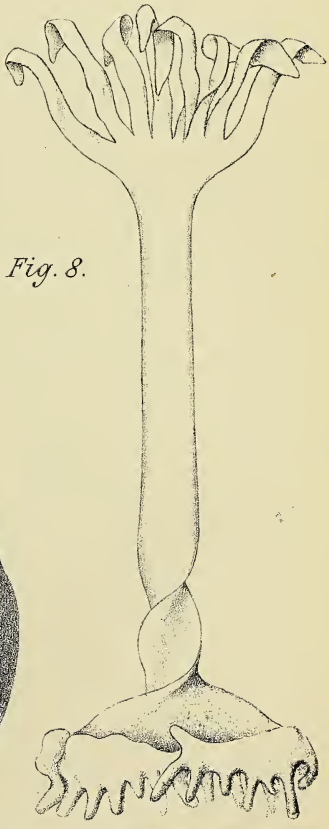

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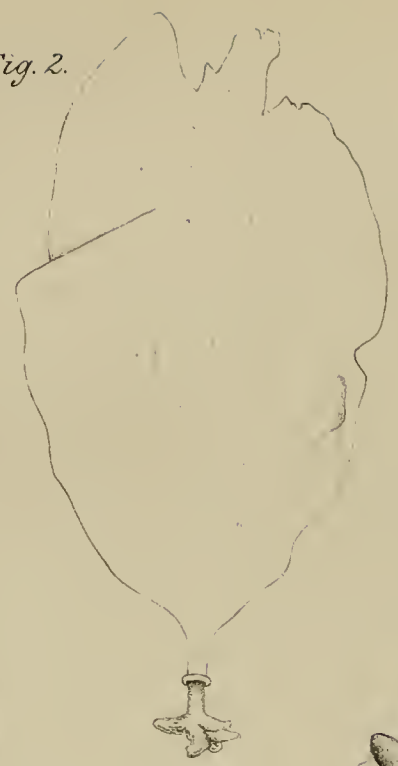

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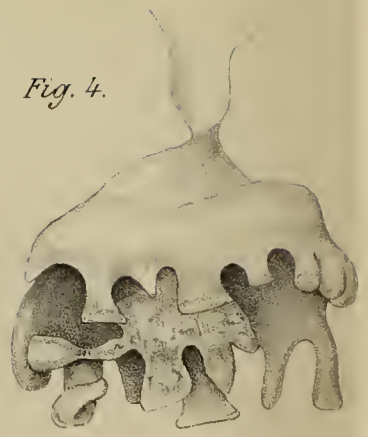

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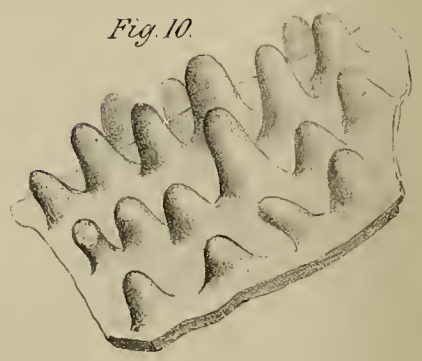

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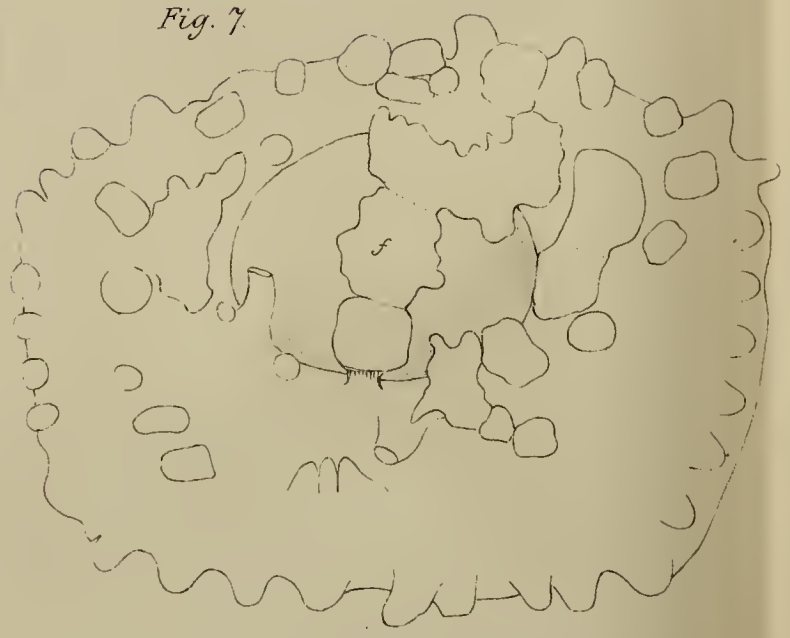

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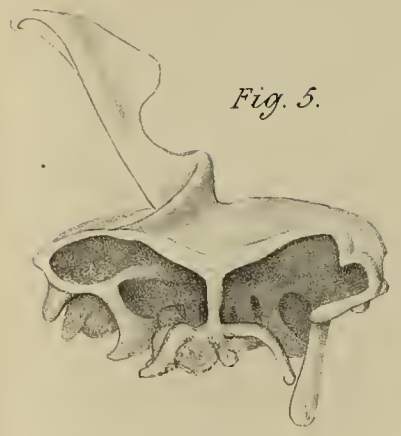

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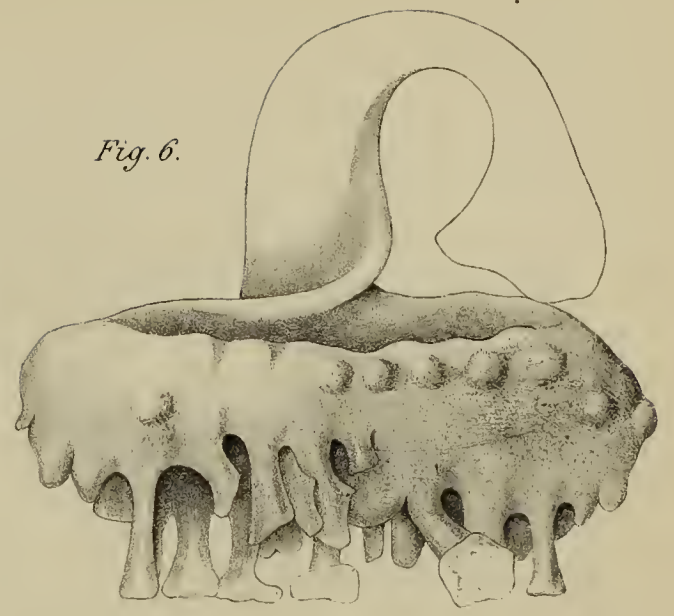

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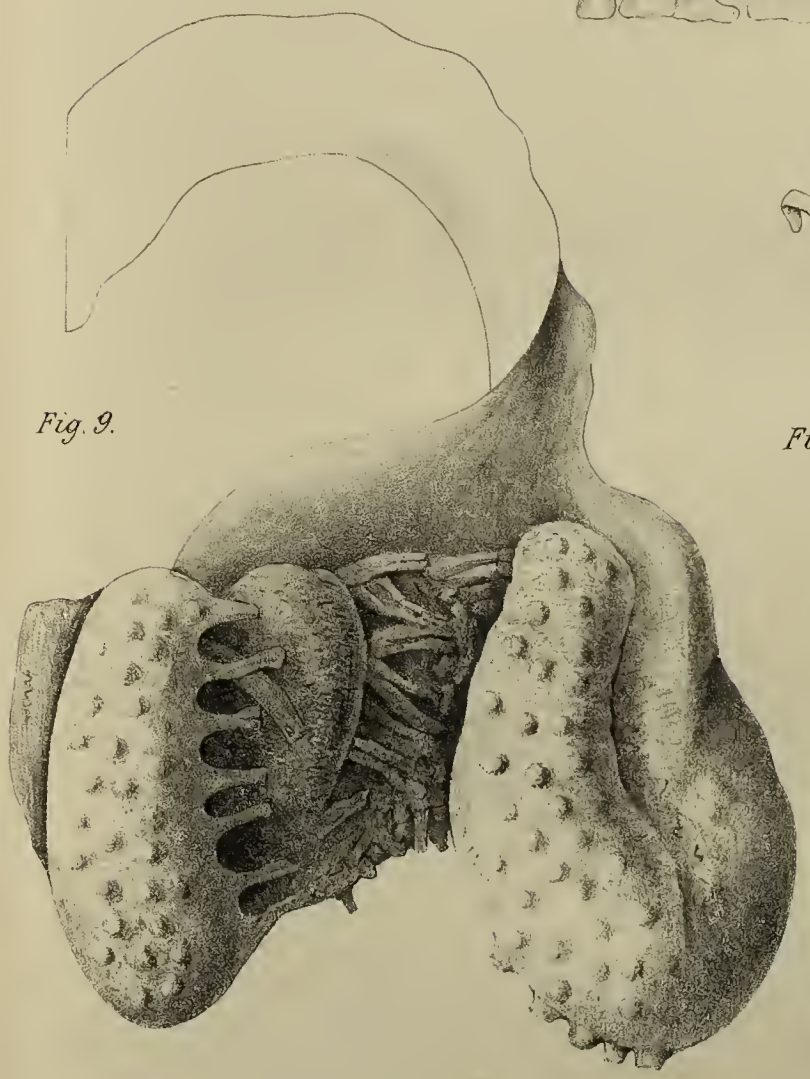

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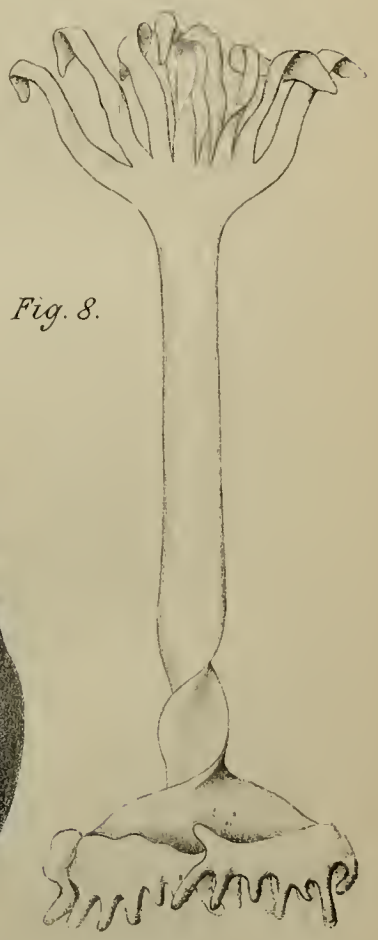

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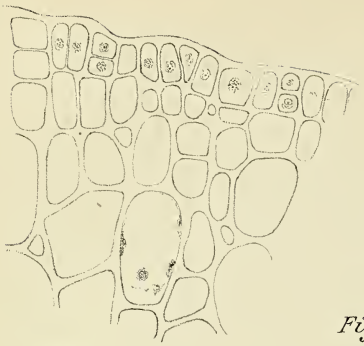

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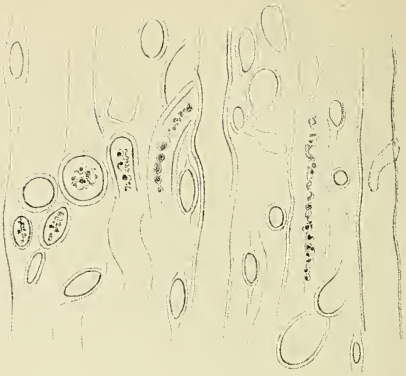

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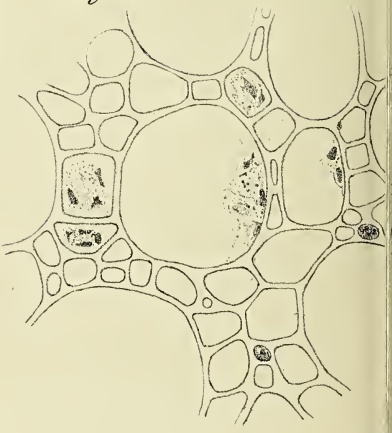

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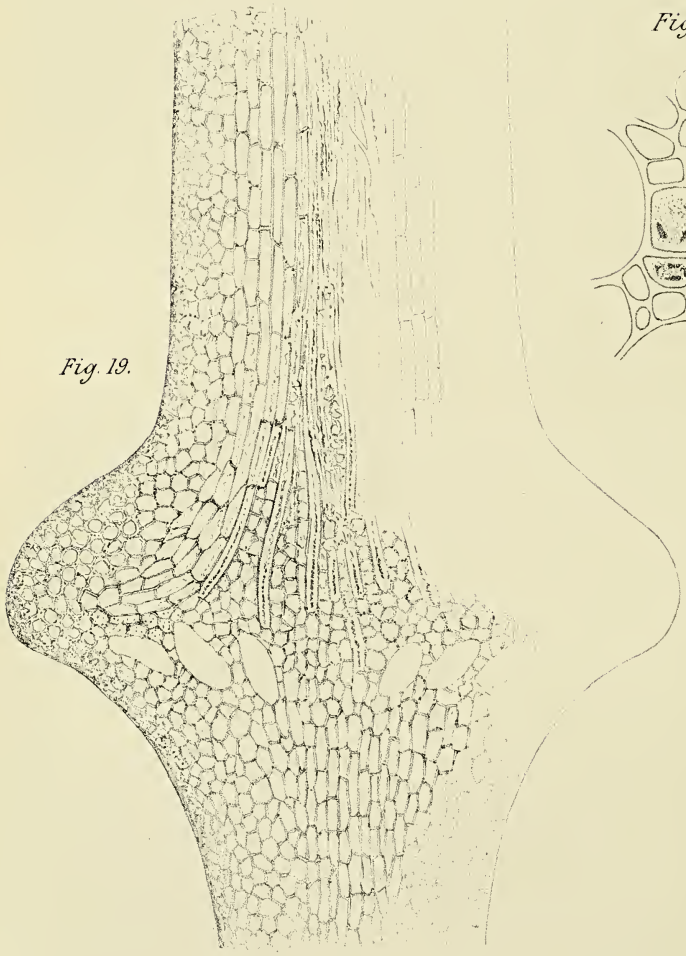

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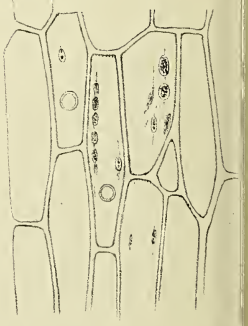

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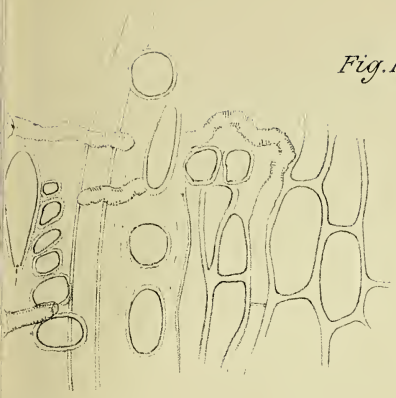

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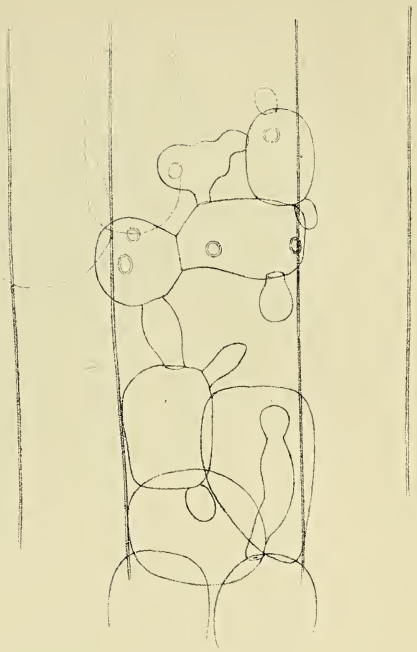

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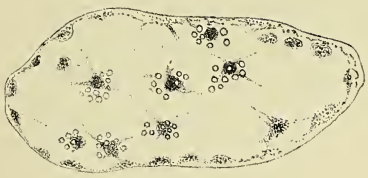

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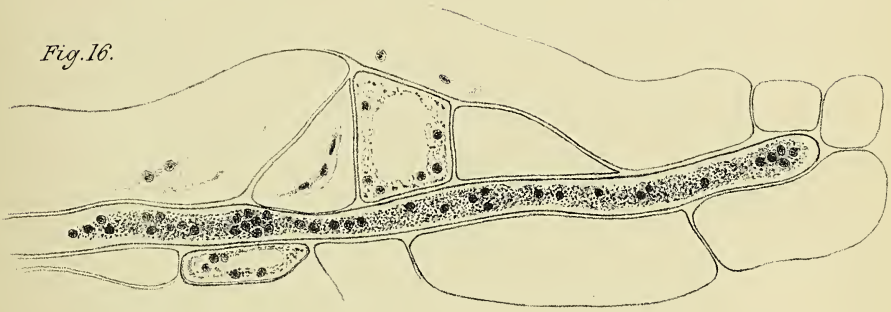

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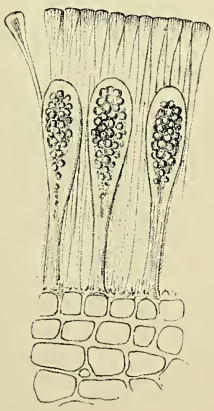

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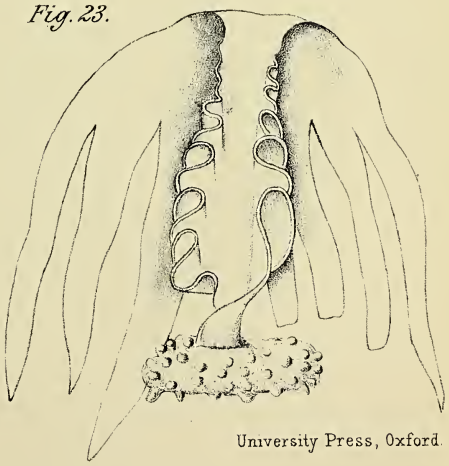

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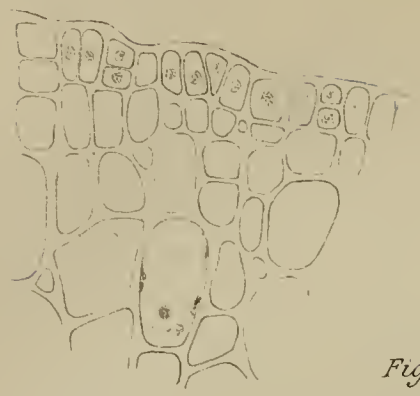

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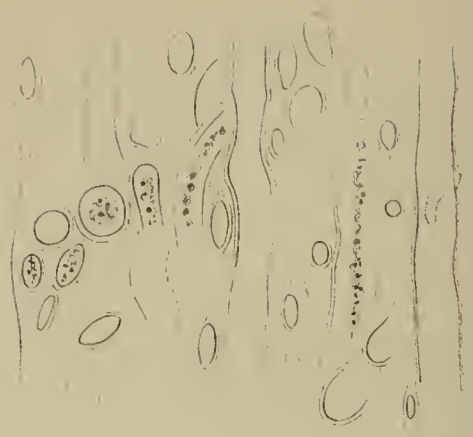

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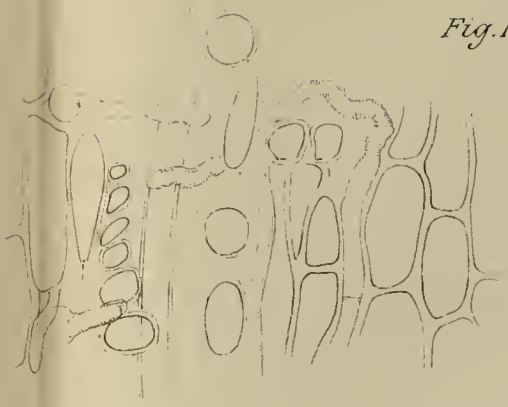

Fig. 13.

Fig. 14.

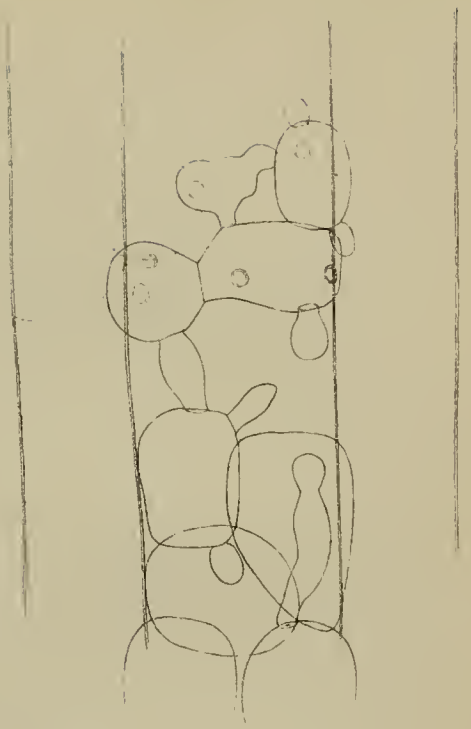

Fig. 15.

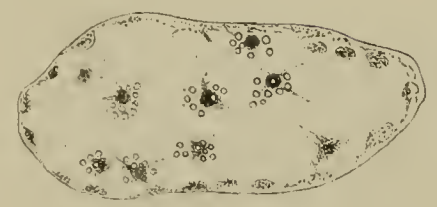

Fig. 17.

Fig. 16.

Fig. 19.

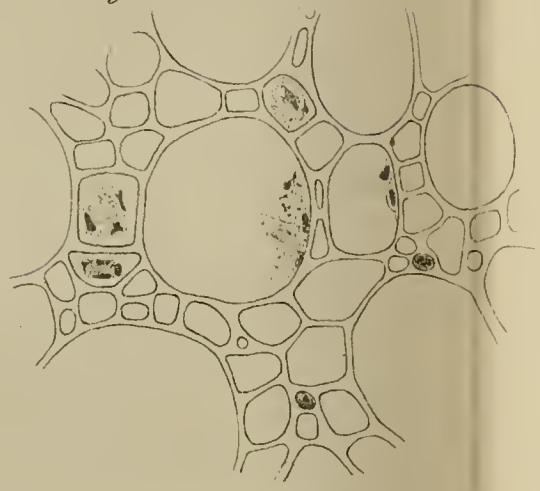

Fig. 20.

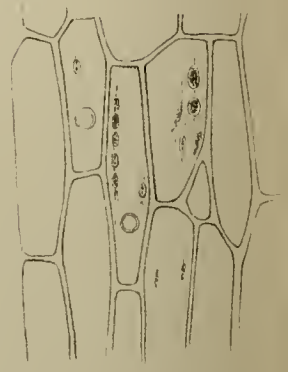

Fig. 18.

Fig. 21.

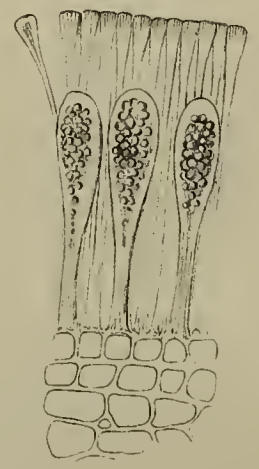

Fig. 22.

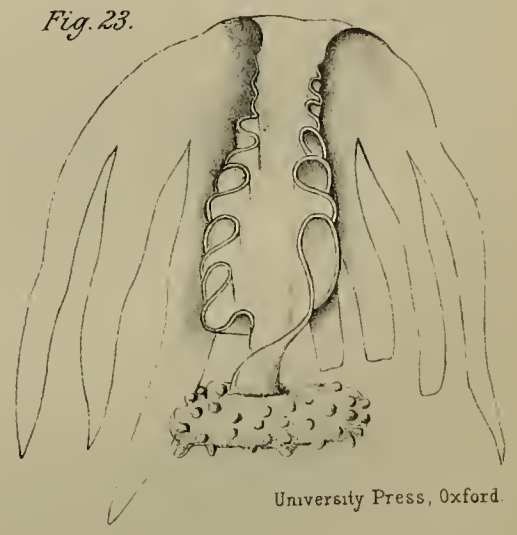

Fig. 23.

C.A Barber del.

University Press, Oxford.

BARBER.—ON LAMINARIA BULBOSA, Lamour.

The Chemistry of Chlorophyll.

BY

EDWARD SCHUNCK, Ph.D., F.R.S., F.C.S.

With Plate VII.

I PROPOSE in the following pages to give a short account of the present state of our knowledge on the chemistry of chlorophyll, and shall avail myself of this opportunity to add a few new facts to the stock already accumulated.

The subject of chlorophyll is one of considerable interest to the chemist; to the botanist and the physiologist it is not only interesting, but also highly important, since there can be no doubt that chlorophyll plays a part in the process of assimilation going on in the vegetable organism. In what manner it assists in the process has not yet, it is true, been exactly ascertained; nevertheless it will hardly be denied that an accurate knowledge of the physical and chemical properties of the substance is calculated to throw some light on its functions, though even, when in possession of such knowledge, the obscurity in which the matter is involved might possibly not be entirely dispelled. Considering the vast amount of labour bestowed by physicists and chemists on the study of chlorophyll, it is surprising how little we really know of the subject. I shall endeavour to explain in the sequel to what this want of success on the part of investigators is due. Several new observers have lately entered the field, and we may therefore look forward to important discoveries in the near future; in the mean time a

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review of what has already been done may prove of interest to the readers of this journal, should it merely serve to show how defective our knowledge is, and how much still remains to be discovered.

What is Chlorophyll?

Before commencing the discussion of any subject it is desirable to define precisely what the subject comprises, what are its limits, and in what sense terms relating to it are employed. The subject to be considered being the chemistry of chlorophyll, the question naturally arises: What is chlorophyll? To this question a physicist, a chemist, and a physiologist might return different answers. Pelletier and Caventou, who invented the term chlorophyll, express themselves as follows:—'Il suit des faits contenus dans cette notice, que la matière verte des végétaux, improprement appelée fécule ou résine, est une substance particulière qui doit être classée parmi les substances végétales très hydrogenées; qu'elle se rapproche de plusieurs matières colorantes, telles que celle de l'orcanette, du curcuma, du santal rouge, et qu'elle mérite, par ses propriétés et le rôle qu'elle joue dans l'économie végétale, d'être considérée comme un principe immédiat des végétaux. Nous proposons de lui donner le nom de *chlorophylle*[1].' It is evident therefore that Pelletier and Caventou considered chlorophyll to be simply an organic colouring matter, a body *sui generis* like indigo or alizarin, but distinguished by its green colour, and their definition should, I think, be adhered to. Some later chemists have given a wider meaning to the term chlorophyll, and made it apply to the sum of the coloured constituents of green leaves, soluble in alcohol and ether, but insoluble in water; and it has accordingly been proposed to call that constituent, the colour of which inclines more to blue, *kyanophyll*, while that constituent or group of constituents which gives solutions of a yellow or greenish-yellow tint, should be named *xanthophyll*. In works

[1] Annales de Chimie et de Physique, IX. 194.

on vegetable physiology the term chlorophyll is sometimes applied to the complex of substances contained in living green cells which take part in the process of assimilation, and of which the colouring matter constitutes a portion; and chemists, following the example of physiologists in giving a name to the whole which should have been confined to one part, have been led to ascribe to chlorophyll properties which no mere chemical substance can possibly possess. Only a few years ago Regnard[1] endeavoured to prove that chlorophyll when dissolved in alcohol, and therefore completely out of the range of influences prevailing in the vegetable cell, was able to decompose carbonic acid and evolve oxygen on exposure to sun-light. Pringsheim[2] has shown that Regnard's conclusions were erroneous. The proof was, however, hardly needed, since no chemist need be told that it is impossible for a substance like chlorophyll, after separation from the organism of which it once formed a part, to effect the decomposition of carbonic acid with evolution of oxygen, unless indeed we suppose that it carries with it into solution a portion of the vitality of its original surroundings, which I imagine no physiologist would allow to be possible.

I may say then, in order to avoid misconception, that in using the term chlorophyll I mean simply the substance—or it may be mixture of substances—to which the pure green colour of ordinary healthy leaves and other vegetable organs is due.

Attempts to isolate Chlorophyll.

In endeavouring to separate chlorophyll from the impurities accompanying it in the extracts prepared from leaves, the older chemists assumed that chlorophyll was a body of very stable character, and they consequently, for the most part, employed strong acids as a means of purification. Now chlo-

[1] Comptes Rendus, Dec. 14, 1885.

[2] Ber. d. Deutschen Bot. Gesellschaft, 1886, IV. 11.

rophyll is very sensitive to the action of acids. On adding an acid, however weak, to a solution of chlorophyll, the colour of the solution changes more or less rapidly from bright green to olive, and the original colour cannot be restored, indicating a complete alteration, though not of course an entire destruction, of the colouring matter. Berzelius, Mulder, Morot, and Frémy, who all employed processes for preparing chlorophyll involving the use of hydrochloric acid, really obtained products resulting from its decomposition, and it is therefore unnecessary to make any further reference to their labours at present.

A few simple experiments should convince an unprejudiced observer that chlorophyll undergoes an entire change under the influence of acids. Nevertheless we still find it asserted occasionally that chlorophyll remains unaltered in the presence of even strong acids. In a memoir published in 1884 Hansen affirms that pure chlorophyll is not essentially changed by the action of sulphuric or hydrochloric acid, and he is of opinion that the product obtained from impure solutions of chlorophyll by contact with acids is not a product of decomposition of the colouring matter, but a mixture of unknown substances formed by the action of acids on the complex alcoholic vegetable extract. In holding this opinion, however, the author, I think, stands almost alone.

Considering the ease and rapidity with which, as is well known to all who have worked with it, chlorophyll is destroyed when its solutions are exposed to air and sunlight, it may appear strange that the colouring matter should not be completely destroyed, instead of being merely modified or altered by energetic agents, such as sulphuric or hydrochloric acid. In fact, however, chlorophyll is not merely modified by the action of these acids, it is completely metamorphosed, yielding products of an exceedingly stable character, products which remain unchanged when exposed to influences which would rapidly destroy the mother-substance, one of the most singular facts connected with the chemistry of chlorophyll.

In a memoir on chlorophyll by M. Arm. Gautier[1], the author describes a method of preparing pure chlorophyll depending on the use of neutral solvents, such as alcohol and ether, along with animal charcoal. The substance was obtained in distinct crystals of an intense green colour, the properties of which, as described by M. Gautier, are such as would probably belong to pure chlorophyll. Referring, however, to the chlorophyllan of Hoppe-Seyler, the discovery of which had been announced a short time previously, the author arrives at the conclusion that it is identical with his crystallised chlorophyll. If so, the latter must have been, as Hoppe-Seyler's chlorophyllan is acknowleged to be, a derivative of chlorophyll, not the pure colouring matter itself.

Hansen[2], following Gautier's directions, did not succeed in obtaining the product described by the latter, and therefore devised a new process for preparing the colouring matter. The essential part of his process consists in the treatment of the residue left on evaporation of an alcoholic extract of young wheat-leaves with boiling caustic soda lye. By this means the fat accompanying the chlorophyll is saponified, and the mixture of soap with other substances having been extracted with petroleum ether in order to remove a yellow colouring matter, then with ordinary ether, is lastly treated with a mixture of alcohol and ether, which dissolves the green colouring matter. The latter is left on evaporation of the solvent in the shape of sphæro-crystals of a dark green colour, the general properties of which are described by the author. The interesting memoir of Hansen forms a valuable contribution to the chemistry of chlorophyll. I am unable, however, to accept the author's conclusions without reserve. The product obtained by him, to which he gives the name of 'chlorophyll-green,' is easily soluble in water, and differs therefore essentially from ordinary chlorophyll, which is insoluble in water, though in most other respects it agrees with the latter.

[1] Comptes Rendus, LXXXIX. 861.

[2] Arbeiten d. Bot. Instituts in Würzburg, III. 123, 430.

Looking at the method of preparation one would be inclined to suspect the presence of sodium in chlorophyll-green; in a later memoir, indeed, Hansen admits that his product is a sodium compound, the sodium being removable by acids; but he does not describe the substance left behind by the acid. The latter, i.e. the liberated colouring matter, is, he admits, like chlorophyll itself, easily altered by strong acids, for which reason it is advisable to use a weak acid, such as boric acid, not sulphuric or hydrochloric acid, for the removal of the sodium. Any one not intimately acquainted with the subject would be inclined to infer, from what has been stated, that Hansen's product, though not itself chlorophyll, is at least a sodium compound of chlorophyll, and that by careful treatment of the compound the colouring matter could be isolated. I do not, however, believe this to be the case. My own experiments lead me to believe that by the action of caustic alkali chlorophyll undergoes a change, which is not indeed apparent to the eye, but which manifests itself when the alkaline chlorophyll is submitted to the action of acids. I have very little doubt that, when Hansen comes to investigate the action of strong acids on his compound he will obtain a product differing from that due to the action of acid on untreated chlorophyll. I shall return to this part of the subject presently.

The general conclusion at which I arrive is this—that chlorophyll has not hitherto been obtained in such a state of purity as to enable us to describe its physical and chemical properties. That it can never be isolated I will not undertake to say, but the difficulties, in consequence of its great liability to change, will be considerable. To reconstruct chlorophyll from its products of decomposition, when these are all known, would perhaps be a task more easily accomplished. Whether, when it has been isolated or reconstructed, it will be found to assume a crystalline form, cannot of course be foretold; but I am inclined to think, that as it exists in the plant, it is amorphous.

Physical and Chemical Properties of Chlorophyll.

If my views are correct it follows that our knowledge of the physical and chemical properties of chlorophyll must be limited. Of a body which can only be obtained in a state of solution, and which is changed or decomposed on attempting to isolate it, we can know but little. If it were possible to obtain a solution of chlorophyll containing no other substance, or at least no other coloured constituent, we should be better off; but we are obliged to content ourselves with treating leaves with some appropriate solvent, and drawing more or less correct conclusions from the behaviour of the solution, which in no case is quite free from foreign substances interfering with the chlorophyll-reactions.

Professor Stokes and others have attempted to purify chlorophyll by agitating alcoholic leaf-extracts with carbon disulphide or benzol, but, as might be expected, with only partial success, since no complete separation of two substances contained in the same solution can be effected by agitating the solution with some liquid, in which one of the two is more soluble than the other; the two solvents taking up both substances, though in different relative proportions. A solution of chlorophyll of sufficient purity for some purposes may be obtained by mixing an alcoholic extract of grass with about twice its volume of water, and then agitating the milky liquid with ordinary ether or petroleum ether. The latter takes up the chlorophyll along with other substances, a quantity of yellow colouring matters and other impurities being left in solution in the lower watery stratum.

Most observers agree in stating that chlorophyll is insoluble in water. Hansen has, however, endeavoured to prove that, when pure, it is really soluble in water, the insolubility usually observed being, according to him, due to its combination with fatty matter in the vegetable organism. Chlorophyll is soluble in alcohol, ether, chloroform, carbon disulphide, ethereal and fatty oils, and similar menstrua. These solutions show the well-known bright green colour and red fluorescence as well as

the peculiar absorption-spectrum about which so much has been written, and which need not be here described.

There can be little doubt that chlorophyll contains nitrogen in addition to carbon, hydrogen, and oxygen, but the percentage is certainly not large. How widely the analyses of so-called pure (crystallised) chlorophyll differ may be seen on comparing the two latest determinations of its composition, which gave the following numbers :—

	Gautier.	Hansen.
Carbon . .	73·97 %	67·26 %
Hydrogen . .	9·80 %	10·63 %
Nitrogen . .	4·15 %	5·120 %[1]
Ash . . .	1·75 %	—

It is evident that the substances, the composition of which is represented by these two analyses, taking for granted that each was pure, could not have been one and the same.

That iron, in some form or other, is an essential constituent of chlorophyll has been repeatedly asserted and as often denied. The uncertainty in this respect is of course due to our being unable to obtain chlorophyll in a state of purity. When a solution of chlorophyll is evaporated to dryness, and the residue is incinerated, the ash is always found to contain a minute quantity of ferric oxide; but whether the latter was derived from the chlorophyll or from some other substance accompanying it and following it into solution must remain doubtful. There is much to be said on both sides of the question, but on the whole I incline to the opinion that iron is not an essential constituent of chlorophyll.

Most of those who have worked with chlorophyll agree in stating that, when burnt, it leaves an ash containing phosphates. When the residue left on evaporation of an ethereal solution of chlorophyll, prepared as above described, is incinerated, it leaves an ash containing a little ferric oxide and a relatively large quantity of calcium and magnesium phosphates. I in-

[1] These were the calculated numbers after deducting the ash, which amounted to 10·76 %, and consisted partly of sodium carbonate.

variably found the ash to have an acid reaction due to the presence of phosphoric acid, or rather of an acid phosphate, a fact, I believe, not previously noticed. These phosphates must have originally existed in a state of combination, the compound or compounds being soluble in alcohol and ether; and if chlorophyll be, as Hoppe-Seyler thinks, a kind of lecithin, the presence of phosphoric acid or phosphates in the ash would be easily explained; but here the usual doubts arise, since we cannot tell whether the phosphates may not have been derived from something else than chlorophyll. I shall reserve the few remarks that I have to make as to the probable constitution of chlorophyll for another paragraph.

Absorption-Spectrum of Chlorophyll.

The characteristic phenomena seen when light after passing through a solution of chlorophyll is examined with a prism have been so frequently described, and are so well known, that it would seem to be unnecessary to add anything to the statements of the many eminent observers who have made them the subject of study. A few remarks on the bands at the more refrangible end of the spectrum may, however, not be out of place. The band in the green, usually named band *IV*, is sometimes represented as very faint, sometimes as rather dark,—a circumstance which is easily explained. The purer the chlorophyll under examination the fainter is this band; when decomposition or change commences, more especially in presence of an acid, then this band becomes darker by degrees, until at last it appears nearly as dark as the band in the red. It is just possible, therefore, that with a solution of chemically pure chlorophyll this band might not be seen at all. Much controversy has taken place regarding the broad indistinct bands at the blue end of the ordinary chlorophyll-spectrum, which are only seen by sunlight and are distinguished as bands *V* and *VI*.[1] Some observers consider these as true chloro-

[1] The notation employed for the bands of the chlorophyll spectrum is that found in German works on the subject.

phyll-bands, others are of opinion that they belong to a yellow colouring matter accompanying chlorophyll, and generally called xanthophyll. Kraus[1], who has paid much attention to this part of the subject, states that he succeeded by treating ordinary alcoholic chlorophyll-solutions with benzol in obtaining two colouring matters, one of which gives yellow non-fluorescent solutions with two absorption-bands at the blue end of the spectrum (xanthophyll), the other bluish-green fluorescent solutions showing, along with the usual bands at the red end, two absorption-bands at the blue end, but not in the same place as those of the other colouring matter (kyanophyll). R. Sachsse [2] repeated Kraus's experiment, using benzin from petroleum, but failed in obtaining a solution of the yellow colouring matter so free from the other as not to show the first chlorophyll-band; this band always appearing when the solution was sufficiently concentrated. In my opinion the bands at the blue end of the spectrum do not belong to chlorophyll,—adopting for the latter the definition with which I started,—but to yellow colouring matters associated with it. My opinion is partly founded on the fact that it is possible to isolate a colouring matter from leaves in regular lustrous crystals, which gives yellow solutions showing two distinct bands in the blue when sufficiently dilute, but no bands whatever in the red, yellow, or green, however concentrated they may be. It is probable that ordinary chlorophyll-solutions contain several yellow colouring matters in addition to those giving definite spectra.

Is Chlorophyll a Homogeneous Substance, or does it consist of Several Substances having very Similar Properties?

This question may be here referred to, because the opinion that chlorophyll is a mixture of several substances is founded principally on observation of its absorption-spectrum. With

[1] Zur Kenntniss d. Chlorophyllfarbstoffe. Stuttgart, 1872.

[2] Die Chemie u. Physiologie d. Farbstoffe, u. s. w. Leipzig, 1877.

reference to this question Professor Stokes[1] says: 'I find the chlorophyll of land-plants to be a mixture of four substances, two green and two yellow, all possessing highly distinctive optical properties. The green substances yield solutions exhibiting a strong red fluorescence, the yellow substances do not. The four substances are soluble in the same solvents, and three of them are extremely easily decomposed by acids or even acid salts; but by proper treatment each may be obtained in a state of very approximate isolation, so far at least as coloured substances are concerned. . . . Green sea-weeds agree with land-plants except as to the relative proportion of the substances present; but in olive-coloured sea-weeds the second green substance is replaced by a third green substance, and the first yellow substance by a third yellow substance, to the presence of which the dull colour of those plants is due.' Mr. Sorby's experiments confirm those of Professor Stokes. According to Mr. Sorby[2]—whose definition of chlorophyll is the same as that which I have given—the chlorophyll of land-plants is a mixture of two substances—'blue chlorophyll' and 'yellow chlorophyll'—while sea-weeds contain two colouring matters belonging to the chlorophyll-group, blue chlorophyll and chlorofucin, the latter replacing the yellow chlorophyll of land-plants. In order to separate these substances one from the other Mr. Sorby agitates alcoholic extracts holding two or more of them in solution with other solvents, such as carbon disulphide and benzol. This method, though it may effect an approximate separation of several substances, having distinct absorption-spectra, can never, when no other means are employed, lead to the isolation of a chemically pure substance. No chemist, moreover, can rely absolutely on the absorption-spectrum of a compound as a means of identification; other tests must be applied as well, and the behaviour of the substance in more than one direction must be examined before complete

[1] Proceedings of the Royal Society, XIII. 144.
[2] Ibid. XXI. 451.

certainty is arrived at. Still, I do not deny that chlorophyll—using the term in the same sense as Mr. Sorby does—may consist of several closely-allied substances; indeed some of my own experiments on the derivation of chlorophyll seem to countenance this view.

Derivatives of Chlorophyll.

Most observers who have taken up the subject of chlorophyll agree in considering it to be a body the molecules of which are in a state of unstable equilibrium, any disturbance of the equilibrium causing the molecules to re-arrange themselves so as to form compounds of a more stable character. External influences of an apparently slight character cause it to undergo considerable change, so much so that it may be considered liable to spontaneous decomposition. To this circumstance the difficulty of isolating it and ascertaining its properties and composition is mainly attributable. Chlorophyll is probably a body of complex constitution and high atomic weight, such as might be expected in the case of a body playing so important a part in the vegetable economy. When difficulties, such as here present themselves, are met with, the founders of modern organic chemistry have laid it down as a rule that the only way to arrive at definite conclusions is to submit the body to be examined to a definite process of decomposition, or to several such processes, and to ascertain the exact nature and composition of the products resulting therefrom. When this has been done the fragments resulting from the splitting up of the complex may be recombined, in theory at least, if not actually, so as to enable us to understand the constitution of the original compound. This is the method which, as regards chlorophyll, has been applied with more or less success by Frémy, Hoppe-Seyler, and others, and it is the one which I have endeavoured to carry out in my experiments. Our knowledge of chlorophyll-derivatives is still very incomplete; indeed, we may say that their study has only just commenced, so that a short account will suffice to

give an idea of what has up to the present time been accomplished on this field of inquiry. After describing the products formed in the processes of decomposition to which chlorophyll has hitherto been submitted, I shall give an account of a peculiar reaction, the study of which may possibly throw some light on the constitution of chlorophyll.

The Spontaneous Decomposition of Chlorophyll and its Products.

The bodies described by Hoppe-Seyler, to which I propose to refer in this paragraph, are acknowledged by their discoverer to be products of decomposition; but since he does not name the agency to which he supposes the decomposition to be due, I have used the word spontaneous in connection with them, putting on one side for a time the fact that a solution of chlorophyll, when light and air are excluded, may be kept unchanged for any length of time.

By extracting fresh grass, which had previously been washed with ether in order to remove the wax covering the epidermis of the leaves, with boiling absolute alcohol, allowing the extract to stand for twenty-four hours, filtering, evaporating spontaneously, and treating the crystalline residue which was left with cold alcohol, then recrystallising from boiling alcohol and from ether, Hoppe-Seyler[1] obtained a substance which he named 'chlorophyllan,' and of which he gives the following description:—'It separates on evaporation of its ethereal solution in spherical grains and crusts consisting of sickle-shaped crystals like those of palmitic acid, which are often grouped together in rosettes and are dark green with a slight metallic lustre by reflected light, brown by transmitted light. The substance has the consistence of bees-wax, and adheres so tenaciously to glass or metal that it cannot again be separated except by redissolving it. It melts at a temperature above 110°C. to a black liquid, which on further heating burns with a luminous flame, leaving a coal which burns with difficulty and

[1] Zeitschrift f. Physiologische Chemie, III. 339, IV. 193, V. 75.

contains phosphoric acid and magnesium. Chlorophyllan is easily soluble in common ether, benzol, chloroform, and petroleum ether. The ethereal solution shows the characteristic absorption between the lines *B* and *C* even when exceedingly dilute. All the solutions show an intense red fluorescence, such as the alcoholic and ethereal extracts of green plants possess; but they differ from the latter in having an olive-green colour like that of plant-extracts after exposure for some time to sunlight, while fresh plant-extracts show the fine bluish-green tint so pleasing to the eye. Moreover, both the absorption-bands between *D* and *F* are much darker and wider than in fresh plant-extracts, in which they are only faintly indicated, but in which they appear with great intensity on exposure to sunlight. Hence the author concludes that chlorophyllan does not exist as such in plants, but is probably formed in the course of the treatment described. The analysis of chlorophyllan gave C 73·34, H 9·72, N 5·68, P 1·38, Mg 0·34 in hundred parts, numbers which do not differ very much from those obtained by Gautier for his crystallised chlorophyll. By treatment with boiling alcoholic potash, chlorophyllan is decomposed, yielding an acid which the discoverer calls chlorophyllanic acid, and which is obtained in bluish-black, lustrous, rhombohedral crystals. Its ethereal solution shows a dark absorption-band between *B* and *C*, another a little paler between *E* and *F*, and between these two three narrow bands of different intensities. Chlorophyllanic acid is not the only product formed by the action of alcoholic potash on chlorophyllan; glycerin-phosphoric acid, and a base supposed to be choline, were also discovered among the products. Hence Hoppe-Seyler infers that chlorophyllan is probably a compound of ordinary lecithin, or is perhaps itself a lecithin in which glycerin and choline, are united to phosphoric acid and chlorophyllanic acid. By treatment with potassium hydroxide at a temperature of 290°C., chlorophyllan undergoes a more profound change, yielding a very peculiar substance which the discoverer calls 'dichromatic acid.' It contains no nitrogen, the nitrogen of the chlorophyllan having escaped in the shape of some volatile

base by the action of the alkali. The solutions of the acid have a pink or purple colour, and possess very peculiar optical properties. The substance is, however, of interest only to the chemist and the physicist, its connection with chlorophyll being remote.

In his memoir on the change of refrangibility of light, Professor Stokes[1] alludes to what I presume he considered to be a derivative of chlorophyll, and which he calls 'modified chlorophyll,' the words he uses being as follows: 'This type was rather ideal than actual, being derived from a comparison of different cases until it seemed to be realised in the case of a fluid obtained by redissolving in alcohol a crust which had formed itself at the bottom of a test-tube containing leaf-green. The principle to which the peculiar absorption of such a fluid seems due may be called modified leaf-green. The fluid itself is not green, but olive-coloured, becoming red at great thicknesses.' Professor Stokes then proceeds to give an account of the absorption-spectrum of this substance, but has not, so far as I know, alluded to the matter again. The subject has, however, given rise to much discussion, opinions being divided as to what modified chlorophyll really is; some observers thinking that it is chlorophyll slightly altered perhaps, not chemically changed, others that it is a product of the action of acids on chlorophyll. I mention it here because it seems to belong to the same class of bodies as Hoppe-Seyler's chlorophyllan, the formation of which is due, or is supposed to be due, to the spontaneous decomposition of chlorophyll.

To the same class belong probably several of the crystalline pigments observed by Borodin[2] on examining alcoholic extracts of the leaves of various plants under the microscope. Most of the pigments described by him belong, however, to the class of yellow-colouring matters which are always found accompanying the chlorophyll of leaves, and of which so little is known.

[1] Philosophical Transactions for 1852, p. 487.

[2] Bulletin de l'Académie Impériale des Sciences de St. Pétersbourg, t. XXVII. pp. 328, 350. 1883.

The Decomposition of Chlorophyll by Acids and the Products formed thereby.

A few simple experiments should suffice to convince any one conversant with the chemistry of plants that by the action of acids chlorophyll undergoes a complete change. If a small quantity of hydrochloric acid be added to an alcoholic or ethereal solution of chlorophyll, the colour of the solution is completely altered, and the absorption-bands are seen to be different in number and position; the change too is a permanent one, for the original colour and the original absorption-spectrum cannot be restored by the addition of an excess of alkali. The colour, moreover, though not so brilliant as before, is now remarkably stable under ordinary conditions, presenting in this respect a marked contrast to the bright colour of the original chlorophyll-solution which disappears rapidly in sunlight. To an unprejudiced observer such facts alone suffice to prove that here a marked change of chemical properties has taken place of a kind, such as workers with complex organic substances are familiar with; and yet the alterability of chlorophyll by acids has by some observers been completely denied or ignored. Unfortunately the subject of chlorophyll has been too much in the hands of persons unaccustomed to weigh chemical evidence, and too easily satisfied with a superficial examination of chemical and physical properties. The somewhat unfortunate use of the word 'modification' may also have led to confusion and misunderstanding, as so often happens when the same term is employed in different senses. To my mind modified chlorophyll is no longer chlorophyll; to those who think otherwise the proposition—indigo is a modification of chlorophyll—might perhaps prove acceptable. Professor Stokes was the first to point out that the chlorophyll of the earlier observers was in fact a product of decomposition due to the action of acids; he too, I think, first obtained a derivative of chlorophyll in a crystalline form. On referring to the memoirs of

Berzelius[1] and Mulder[2], it will be found that they employed concentrated hydrochloric acid as a means of purifying chlorophyll; it is evident therefore that they worked with a product or products of decomposition, not with unaltered chlorophyll. Berzelius describes three modifications of chlorophyll obtained by him from green leaves, though with regard to one of them he admits that it may have been the product of chemical treatment, and not really have pre-existed in the plant. As regards chlorophyll on the whole, however, Berzelius asserts that it is not destroyed either by acids or alkalis, but rather combines with them in definite proportions. Much here depends on the meaning of the word 'destroy'; the colour of chlorophyll is certainly not destroyed by hydrochloric or sulphuric acid, it is rather heightened by an excess of either of these acids; but an examination of the spectrum of chlorophyll before and after treatment with acid would have shown that a change had taken place. It was the mere similarity in colour that led Berzelius to suppose that the biliverdin of bile was identical with chlorophyll. According to Professor Stokes, the two substances are totally distinct, the solution of biliverdin showing none of the absorption-bands peculiar to chlorophyll. The memoir of Berzelius on chlorophyll contains, however, some observations which are still of some interest, and to which I shall refer hereafter. By the combined action of ether and hydrochloric acid on chlorophyll Frémy obtained two colouring matters, a blue and a yellow one. Since some doubt has been expressed with regard to the conclusions to which he was led by his experiments, I think it best to describe what he observed in his own words. He says, 'Voulant donc séparer les deux matières colorantes qui donnent à la chlorophylle sa couleur verte, j'introduis dans un flacon un liquide composé de 2 parties d'éther et 1 partie d'acide chlorhydrique étendu d'une petite quantité d'eau; j'agite fortement le flacon de manière à saturer l'acide chlorhydrique d'éther. En

[1] Annalen d. Pharm. XXVII. 296.

[2] Journ. f. Pract. Chemie, XXXIII. 478.

soumettant alors à l'action de ce liquide le corps qui provient de la décoloration de la chlorophylle' (an alumina lake of chlorophyll) 'et agitant la liqueur pendant quelques secondes, on voit se produire une réaction bien remarquable; l'éther retient la matière jaune des feuilles et conserve une coloration d'un beau jaune, tandis que l'acide chlorhydrique réagissant sur la partie de la chlorophylle qui a été decolorée, reproduit une substance d'un bleu magnifique. Les deux couleurs de la chlorophylle, le bleu et le jaune, se trouvent donc ainsi isolées et ne peuvent plus se mélanger pour produire une teinte verte, puisqu'elles sont retenues par deux liquides différents, l'éther et la liqueur acide . . . J'ai donné le nom de *phylloxanthine* à la matière jaune soluble dans l'éther, et de *phyllocyanine* à la matière bleue qui reste en dissolution dans la liqueur acide [1].' This is the well-known chlorophyll-reaction which has generally been connected with the name of Frémy, though it had previously been observed by Berzelius as characterising his second modification of chlorophyll. From what Frémy states it has been inferred that he considered chlorophyll to be simply a mixture of a blue and a yellow colouring matter which were separated by his method of treatment; but this has been denied by Frémy himself, who in a subsequent memoir [2] describes some experiments from which he concludes that chlorophyll is a kind of coloured fat, which by saponification splits up into phyllocyanic acid, a substance which yields blue compounds and represents the fatty acid, and phylloxanthin which is yellow and crystalline, and corresponds to the glycerin of ordinary fats. In a third communication to the French Academy [3], Frémy states that phylloxanthin and phyllocyanic acid do not exist in a state of combination in leaves, the latter being in fact present in the form of a potassium salt. The final conclusion at which he arrived is stated as follows: 'Je crois donc que la démonstration est complète, et qu'il m'est permis d'affirmer aujourd'hui que la matière colorante des feuilles est un mélange de phylloxanthine

[1] Comptes Rendus, L. 409. [2] Ib. LX . 188. [3] Ib. LXXXIV. 983.

et de phyllocyanate de potasse.' It is certain that nearly all the substances described by Frémy are products of decomposition, formed by the action either of acids or of alkalis on chlorophyll.

Filhol[1] made a step in advance by showing, in accordance with the previous statement of Professor Stokes, that chlorophyll in solution is very easily decomposed by acids, even weak acids, such as acetic, sufficing for the purpose and yielding products which after removal of the acid do not, when dissolved together in ether, afford solutions showing the bright green colour of the original solution. Filhol's description of the 'matière solide brune' which is deposited when an acid is added to an alcoholic solution of chlorophyll shows that it is essentially the same substance as that which, when dissolved in hydrochloric acid, constitutes the phyllocyanin of Frémy, and is probably also identical with the second chlorophyll modification of Berzelius.

In the year 1874, Filhol[2] presented to the French Academy a note on chlorophyll, in which he states that by the action of hydrochloric acid on the chlorophyll of dicotyledonous plants he obtained 'une matière noire amorphe,' while by operating in the same manner on the chlorophyll from monocotyledons he obtained 'une matière noire cristallisable.' The crystals of the latter substance are only visible under the microscope; they form little tufts consisting of fine needles. This is perhaps the first time that a crystalline derivative of chlorophyll is mentioned in any publication[3]. After giving a general account of its properties, Filhol states that the solution of his substance in acetic acid acquires a magnificent green colour when it is boiled with the addition of a little

[1] Comptes Rendus, LXVI. 1218.

[2] Ibid. LXXIX. 612.

[3] Several years ago, when my attention was first directed to this subject, Professor Stokes very kindly wrote me several letters giving an account of his researches on chlorophyll conducted long previously. In one letter he describes a substance crystallising in rosettes, nearly opaque, which he identifies with Frémy's phyllocyanin, without, however, referring to any publication in which the product was described.

acetate of copper or acetate of zinc. This reaction, lately rediscovered by Tschirch and by myself, is characteristic of Frémy's phyllocyanin, with which Filhol's 'matière noire crystallisable' must therefore have been identical.

Every one who has worked at the chemistry of plants must have observed the peculiar change of colour which takes place when fresh green leaves are treated with dilute acids. As the acid penetrates into the interior of the leaves the bright green colour changes to olive, at the same time losing greatly in intensity. This change is due, in the opinion of most observers, to the decomposition of the chlorophyll by the acid. When acidified leaves are extracted with boiling alcohol a greenish-yellow solution is obtained, which only a colour-blind person could mistake for an extract of fresh leaves with its lovely green colour. The solution no longer shows the absorption-spectrum of chlorophyll, but that of so-called 'acid chlorophyll,' which is characterised by the appearance of two very dark bands at the more refrangible end in addition to those at the other end of the chlorophyll-spectrum, the latter being at the same time slightly altered as regards position and relative intensity. It is the presence of free acid in some leaves, such as those of the vine and Virginian creeper, that prevents our seeing the normal chlorophyll-spectrum in the extracts of such leaves; the acid re-acts on and changes the chlorophyll during the process of extraction, a change which according to Russell and Lapraik may be prevented by adding calcium carbonate to the bruised leaves before extraction with alcohol and ether. The carbonate of soda which cooks are in the habit of adding to green vegetables before boiling has the effect of preventing the discoloration which would otherwise take place in consequence of the presence of free acid in the leaves.

Those who take a special interest in the subject should refer to the able and elaborate memoir entitled 'A Spectroscopic Study of Chlorophyll by Dr. Russell and Mr. Lapraik[1],'

[1] Journal of the Chemical Society, XLI. 334.

who have given a detailed account of the successive changes observed in the normal chlorophyll-spectrum on the addition of acids to chlorophyll solutions. For those who take only a general interest in the matter the following short account will probably suffice:—If to an ethereal solution of chlorophyll—prepared in the manner above described—contained in a test tube a few drops of hydrochloric acid be added, the colour of the solution changes at once from bright green to yellowish-green. Examined with the spectroscope it will be found that bands I and II have become more distinct than before in consequence of the clearing up of the space between them, while band III has moved further away from the red end appearing at the same time very much paler, and band IV on the other hand has become very much darker; on the solution standing for some days a fifth band (IV *b*) begins to appear between the lines *E* and *F*, becoming gradually as dark as the fourth band, a sign that the action of the acid is completed. The same series of changes occurs when a crystal of tartaric acid is dropped into the ethereal solution and shaken up with it, but a much longer time elapses before the final stage is reached. On adding a quantity of acetic acid to the chlorophyll-solution, no change is observed at first as regards either its colour or its absorption-spectrum; but after standing for some days the solution appears yellowish-green, and now shows the same bands as are produced at once by hydrochloric acid, bands I and II being very distinct, band III very faint, and band IV very dark, the fifth band not appearing at all even after a considerable time. Hence it appears—relying on the results of spectroscopic observation—that by the action of a strong acid chlorophyll undergoes at once a change, which is only brought about after a long time under the influence of a weak acid, while the final effect of the action of a strong acid is not produced at all by a weak acid, a moderately weak acid like tartaric acid acting less rapidly than a strong acid, but more rapidly than a weak one. That the change due to the action of acids is not the result of a process like that of the decomposition of a

coloured lake, which yields up its base to an acid at once, is evident; first because it takes time for completion even with strong acids, and secondly, because—taking the case of the change produced at once in a solution of chlorophyll by a little hydrochloric acid—the original green colour is not restored by an excess of alcoholic soda, as it would probably be were the action a very simple one, like the decomposition of a saline compound by an acid stronger than the one contained in it. Russell and Lapraik come to the conclusion that the change is a molecular, not a chemical one. In this opinion I cannot concur, so far at least as regards the final product of the action of strong acids, which I take to be identical with Frémy's phyllocyanin. As to the initial product of the action of strong acids, which shows only four absorption-bands—Russell and Lapraik limit them to three—I pronounce no opinion, having made no attempt to isolate it or to ascertain its other properties. It may be a mere so-called modification of chlorophyll, or it may be identical with the chlorophyllan of Hoppe-Seyler.

On reading Professor Pringsheim's memoir on chlorophyll [1] it occurred to me that his hypochlorin might represent the initial product of the action of acids on chlorophyll. Professor Pringsheim obtained the substance referred to by acting on green leaves of any kind with dilute hydrochloric acid. After the leaves had been immersed in the acid for some time it was found, on microscopic examination, that masses of a reddish-brown colour had formed on and attached to the chlorophyll-corpuscles, these masses sometimes throwing out long rods mostly bent or twisted and pointed at the ends and having the appearance rather of a crystalloid than of a crystallised substance. This body, or rather the body contained in the chlorophyll-corpuscles from which it is formed by the action of acids, Pringsheim supposes to be the basis of chlorophyll itself—hence the name hypochlorin;—but in what sense this is to be understood is to myself at least

[1] Lichtwirkung u. Chlorophyllfunction in d. Pflanze, Leipzig, 1881.

not quite apparent. Arthur Meyer[1], having examined Pringsheim's hypochlorin with regard to its chemical properties as well as its appearance under the microscope, came to the conclusion that it is identical with Hoppe-Seyler's chlorophyllan.

In several memoirs published in the years 1881 and 1884 Robert Sachsse[2] has given an account of two substances of which he says that they are contained in the mixture known under the name of modified chlorophyll, and which he calls α-phaeochlorophyll and β-phaeochlorophyll respectively. Of these he has given a general description, but as regards their absorption-spectra he merely states that they are nearly the same as that of modified chlorophyll. Both products are amorphous, so that they cannot be identical with Frémy's phyllocyanin, nor with Filhol's 'matière noire,' which are crystalline.

I am inclined to think, after carefully considering what has been written on the subject, that no derivative of chlorophyll showing the absorption-spectrum of Russell and Lapraik's α-chlorophyll has so far been isolated.

I shall now proceed to give an account of my own experiments on the action of acids on chlorophyll[3]. I may state that these experiments do not refer to such products as are due to the action of weak acids on chlorophyll nor to those formed during the first stage of decomposition by strong acids. Some discrepancies may therefore possibly be discovered between my results and those of some other observers.

Fresh green leaves—I prefer grass to any other material—are to be extracted with strong boiling alcohol, and the dark green extract having been poured off from the exhausted leaves is allowed to stand for a day or two, when it deposits a quantity of wax, fatty matter, and other impurities which

[1] Das Chlorophyllkorn, Leipzig, 1883.

[2] Chem. Centralblatt, 1881, pp. 169, 236; ib. 1884, p. 113.

[3] Proceedings of the Royal Society, No. 240, 1885.

had been dissolved along with the colouring matter. The deposit having been filtered off, a current of hydrochloric acid gas is passed through the filtrate. This produces at once a dark green, nearly black voluminous precipitate, which increases in quantity on standing. The precipitate is separated by filtration from the greenish-yellow liquid, containing colouring and other matters extracted along with the chlorophyll, and then washed with alcohol in order to remove these together with the excess of acid. The precipitate contains, mixed with impurities chiefly of a fatty nature, two distinct colouring matters, which are identical with the phyllocyanin and phylloxanthin of Frémy. These names I have seen no reason to change, though they are not perhaps very appropriate. The method which I adopt for separating the two substances is essentially the same as that of Frémy. The crude product of the action of the acid is first treated with ether in which nearly the whole dissolves. The insoluble matter having been filtered off, the filtrate is mixed with about an equal volume of strong hydrochloric acid. The mixture after being well shaken is left to stand, when it separates into two layers, an upper yellowish-green one, containing phylloxanthin, and the greater part of the fatty matters, and a lower dark blue one containing phyllocyanin in combination with hydrochloric acid. The two liquids are separated in the usual way and with as little delay as possible —since on standing the phylloxanthin begins to dissolve in the hydrochloric acid and passes gradually into the lower stratum—and the blue solution is agitated with ether, the process being repeated until the ether takes up no more colour. The solution, after exposure to the air, to allow the ether contained in it to evaporate, is mixed with water which produces a dark blue precipitate. This is filtered off, washed to remove the acid, and then dissolved in boiling glacial acetic acid. This solution gives on cooling a crystalline deposit of phyllocyanin, which is filtered off and recrystallised from boiling acetic acid, finally washed with alcohol and dried. By the process just described I obtained phyllocyanin from ivy leaves, from the

leaves of the common thorn, and from the fronds of *Pteris aquilina*, as well as from grass; no difference could be discovered between the various specimens obtained.

Phyllocyanin is one of the most important of the derivatives of chlorophyll; its properties moreover are very interesting. When dry it has the appearance of a dark blue mass, which may easily be reduced to a fine powder resembling pounded indigo, but without the coppery lustre exhibited by the latter substance when rubbed with a hard body. Examined under the microscope it is found to consist almost entirely of elongated rhomboidal or irregularly six-sided crystalline plates, which are generally opaque, but when very thin are translucent, and then appear olive-coloured by transmitted light. Phyllocyanin is insoluble in water; it dissolves in boiling alcohol, but a great part separates out on the solution cooling in microscopic crystals; it is more soluble in ether, benzol, glacial acetic acid, and carbon disulphide than in alcohol, but the best solvent is chloroform, which takes up large quantities of it, even in the cold. A minute quantity of substance imparts an intense colour to most of these solvents; it is only on diluting largely that the solutions lose their opacity; they then appear of a dull green or olive colour, and show the well-known spectrum of 'acid chlorophyll,' consisting of five absorption-bands; they fluoresce, but not so strongly as solutions of chlorophyll. Phyllocyanin is soluble in aniline, but insoluble in petroleum, ether and ligroin; it contains nitrogen, but is free from sulphur. Phyllocyanin may be heated to 160° C. without change; between 160° and 180° it is, however, completely decomposed, leaving a charred mass of the same volume as the substance taken, which, when further heated, burns away leaving a hardly visible trace of ash, differing in this respect from chlorophyllan, which after burning leaves a quantity of incombustible matter.

Phyllocyanin is soluble in concentrated hydrochloric and sulphuric acids. The solution in hydrochloric acid appears dark blue by day-light, purple in artificial light, and shows a

spectrum differing from that of phyllocyanin and more nearly approaching that of chlorophyll. In some works this spectrum is called the spectrum of phyllocyanin, but it is in fact the spectrum of the compound with hydrochloric acid, phyllocyanin playing towards strong acids the part of a base. It forms, however, only loose combinations with acids; consequently on adding water to a solution in either of the two acids named, it is precipitated unchanged. If the solution in sulphuric acid is left to stand for some time, or if the solution in hydrochloric acid is evaporated to dryness, the phyllocyanin undergoes a change of the same nature as that induced by the action of alkalis. Phyllocyanin shows no tendency to combine with phosphoric, oxalic, tartaric, or citric acid, which is not surprising considering that its character as a base is so little pronounced. Glacial acetic acid acts merely as a solvent, the solution showing nearly the same absorption-spectrum as that in alcohol, ether, and other menstrua. Nitric and chromic acids decompose phyllocyanin, yielding yellow products of no interest.

On passing chlorine gas through a solution of phyllocyanin in chloroform, the colour changes from dull-green to a bright grass-green, like that of a solution of chlorophyll itself; it still shows absorption-bands, but these do not coincide with those of chlorophyll nor with those of phyllocyanin. On continuing to pass chlorine through the solution the colour changes to yellow, and it now shows no trace of absorption-bands; the products of the action are amorphous. Bromine acts in a similar manner.

Any one who has observed the ease and rapidity with which a solution of chlorophyll is bleached on exposure to light and air must be struck with the extraordinary permanence exhibited by phyllocyanin solutions under the same circumstances. A moderately strong solution of phyllocyanin, when exposed to sunlight, retains its colour for a long time, the last trace disappearing only after many weeks' exposure. In order to observe the changes which take place, it is best to take a chloroformic solution of phyllocyanin and expose it

to sunlight in a loosely stoppered bottle, the stopper being occasionally removed, and the contents shaken. The green colour of the solution gradually becomes fainter, the absorption-bands of phyllocyanin still remaining visible. After some time the colour changes to yellow, but the solution still shows a strong band in the red, the other bands having disappeared. At length this band also vanishes, and there is now nothing to be seen but the total obscuration at the blue end of the spectrum which most yellow solutions show. It is the great stability of phyllocyanin as compared with that of chlorophyll which is the cause of the slow disappearance of the colour and absorption-bands of solutions of chlorophyll that have not been carefully prepared. The absorption-bands which in such cases remain even after a prolonged exposure, are due, not to chlorophyll, but to the presence of phyllocyanin, formed either spontaneously or in consequence of the solution containing acid. Chlorophyll and phyllocyanin stand, as regards stability, in the same relation to each other as indican and indigotin; indican being a substance very easily decomposed, whereas indigotin, which is a derivative of indican, is one of the most stable of colouring matters. The change which phyllocyanin undergoes during insolation is doubtless due to oxidation. The process yields two products; one being yellow, amorphous, resinous, soluble in alcohol, insoluble in water; the other is soluble in water, has a strong acid reaction, and reduces Fehling's solution. Both products may be mixtures of several substances. Phyllocyanin is soluble in alkalis, the solutions being green, but there can be not doubt that it is changed by the action of alkali, since the reactions of the substance precipitated on the addition of acid are not those of the original phyllocyanin. The properties of this substance will be described when I come to describe the action of alkalis on chlorophyll.

The behaviour of phyllocyanin towards acids shows that its character is that of a weak base, since it combines only with strong acids yielding unstable compounds which are decomposed by water.

Notwithstanding its nearly neutral character, however, phyllocyanin is capable of yielding compounds of great comparative stability, into which metals and acids, more especially organic acids, enter as constituents. When phyllocyanin is dissolved in boiling glacial acetic acid it crystallises out unchanged on the solution cooling. The same happens when freshly precipitated cupric oxide or zinc oxide is added to a boiling alcoholic solution of phyllocyanin; the solution deposits phyllocyanin and there are no indications of any combination having taken place between the phyllocyanin and the metallic oxide. A very different effect is observed when either of the two oxides is employed along with acetic acid. When cupric oxide is added to a solution of phyllocyanin in boiling acetic acid, the solution acquires at once a deep greenish-blue colour, and it no longer contains uncombined phyllocyanin, for it shows a different spectrum, and on standing it deposits lustrous crystals, which consist of a compound of which phyllocyanin, acetic acid, and copper are essential constituents. If zinc oxide be employed, a similar effect is observed; the liquid acquires an intense green colour, and now contains the corresponding acetate of phyllocyanin and zinc. Similar phenomena are seen when ferrous oxide, manganese oxide, or silver oxide is taken, solutions of various shades of green being obtained, which contain phyllocyanin-compounds; but no similar compounds are formed when potassium, sodium, barium, calcium, magnesium, or lead acetates are employed, for on adding the acetate of any one of these metals to a solution of phyllocyanin in boiling acetic acid, the colour of the latter remains unchanged, and phyllocyanin is deposited just as if no metallic acetate were present. Acetic acid is, however, not the only acid which gives the reaction. If palmitic, stearic, oleic, tartaric, citric, malic, or phosphoric acid be employed, it occurs just as with acetic acid, but in some cases time is required for its completion. Some combinations, contrary to what might have been expected, are without effect; such are cupric oxide and oxalic acid, zinc oxide and oxalic acid, zinc oxide and

tartaric acid, ferrous oxide and tartaric acid. Such of these compounds as do exist have a number of properties in common, though the several classes differ *inter se* in some important particulars. They all dissolve—after having been precipitated by water from the solutions in which they were formed—more or less easily in alcohol, ether, chloroform, benzol, and carbon disulphide; the phyllocyanin manganese acetate differs from the others in being soluble in water. The solutions have a colour varying from grass-green to a fine bluish-green, and they show peculiar spectra. The solutions remain quite unchanged when sulphuretted hydrogen is passed through them; no precipitate is formed, and on evaporation the various compounds are left behind with their original properties unaltered. It is only on incineration that the presence of the metallic constituent is detected, the copper compounds leaving, after being burnt, cupric oxide, the zinc compounds zinc oxide, the iron compounds ferric oxide. They all dissolve in dilute alkaline lyes, and are re-precipitated unchanged on the addition of acetic acid. Of these compounds the zincic group is perhaps the most interesting in consequence of the striking resemblance which they show as regards some of their properties to chlorophyll itself. These compounds yield bright green, strongly fluorescent solutions, which show an absorption-spectrum very like that of chlorophyll as regards the number and relative intensity of the bands; the colour of these solutions soon disappears on exposure to light, though it is more permanent than that of a chlorophyll solution of the same intensity of tint. The zinc compounds are easily decomposed by hydrochloric acid, phyllocyanin being at once reproduced. Zinc oxide is the only oxide which yields a compound with carbonic acid and phyllocyanin; the compound is dark green and semi-crystalline, and may be heated to 150° C. without decomposition. On adding hydrochloric acid to an alcoholic solution of phyllocyanin zinc carbonate and heating, bubbles of gas are seen to escape, the colour of the solution changes to blue, and on now adding water, there is a dark flocculent precipitate which dissolves easily on shaking up with ether,

the solution showing the colour and absorption-bands peculiar to phyllocyanin-solutions. It is evident that the compound is decomposed, the hydrochloric acid combining with the zinc oxide and the phyllocyanin, while the carbonic acid escapes, the phyllocyanin hydrochloride being decomposed on the addition of water. I have already mentioned the fact that Filhol observed a green coloration on adding zinc acetate to a solution of his 'matière noire crystallisable.' The same reaction was obtained by Tschirch on treating chlorophyllan in solution with zinc powder. Both observers must have been working, I imagine, either with phyllocyanin or some closely allied substance. The acid, the presence of which is in my opinion an essential condition of the reaction, consisted in Tschirch's experiment, I rather think, of some fatty acid.

The cupric class of compounds is almost as interesting as the zincic. These compounds give solutions of a brilliant colour inclining more to blue than to green, and showing spectra with four absorption-bands, the position of which varies somewhat according to the acid employed. They are compounds of remarkable stability. If an alcoholic solution of any one of them be mixed with a large quantity of hydrochloric acid and boiled, the colour remains unchanged, and on adding water and then shaking up with ether, the ethereal liquid which rises to the surface shows the same colour and the same spectrum as the original alcoholic solution. Such an alcoholic solution may be exposed in a loosely stoppered bottle to alternate sunlight and diffused daylight for weeks and even months without undergoing any perceptible change, being more stable under these circumstances even than phyllocyanin solutions. That these compounds should exhibit such remarkable stability as compared with the corresponding compounds of zinc is a singular and unaccountable fact. The most beautiful of the cupric series of compounds is the phyllocyanin cupric acetate. It is best prepared by adding cupric acetate to a solution of phyllocyanin in boiling acetic acid. The crystalline mass which separates out on standing is filtered off, treated with dilute hydrochloric acid to remove any excess of cupric acetate

that may be present, and then redissolved in boiling glacial acetic acid. The solution on cooling deposits the compound in crystalline plates, which are elongated, pointed at the ends, of a pale greenish-blue by transmitted, and of a brilliant purple, with a semi-metallic lustre, by reflected light. A solution of this compound in acetic acid imparts very pleasing shades of green to white leather and to wool, silk, or cotton prepared with albumen; it acts as a so-called substantive dye, i.e. one that requires no mordant for its fixation. When the reprehensible practice of adding copper to the vinegar used for pickling vegetables is followed, it is this compound which is formed, imparting to the vegetables the lively green colour which some people admire; vinegar alone turns the colour of vegetables to a greenish-brown in consequence of the formation of phyllocyanin or phylloxanthin. A commercial preparation has lately been introduced to which the name chlorophyll has been given. It consists essentially of one of the cupric compounds just described, as may be seen on comparing the absorption-spectrum of its ethereal solution with that of phyllocyanin cupric acetate.

If it be thought desirable by the collector of plants to preserve the green colour of his specimens he may do so by immersing them for some time in vinegar holding acetate of copper in solution, then taking them out, washing well, and drying as usual. The effect with some plants is extremely pleasing, the green tint of the living leaves being retained; the process, I have no doubt, would tend to preserve the specimens, though the time it would require would probably render it inapplicable in most cases.

The phyllocyanin compounds containing iron yield solutions of a pure green tint like that of chlorophyll, but they are not strikingly fluorescent, and when exposed to sunlight in open vessels they retain their colour for a long time. The ferrous group may be divided into two sub-groups; the first sub-group comprising compounds into which one of the fatty acids—acetic, palmitic, or oleic acid—enters as a constituent; the other sub-group consists of such as are formed by the

action of citric, malic, or phosphoric acid. To each sub-group belongs a distinct spectrum. The ferrous compounds are changed by the action of hydrochloric acid, but without yielding phyllocyanin as a product of decomposition as do the zinc compounds, occupying in this respect, as in most others, a position intermediate between the cupric and zincic groups. That silver should yield a compound with phyllocyanin and acetic acid, and lead should not, is a singular fact, proving, as do other facts that I have mentioned, that phyllocyanin is a substance possessing very peculiar properties.

I have entered into a more detailed description of these compounds of phyllocyanin than would seem to be required on this occasion, because in my opinion chlorophyll itself belongs, for reasons which I shall state presently, to the same class of compounds, though it is not identical with any one and indeed differs widely from most of them.

Reducing agents act in a peculiar manner on phyllocyanin, giving rise to products which cannot be reconverted into phyllocyanin by oxidation, and are therefore not so-called leuco-bodies like indigo-white. When metallic tin is added to a solution of phyllocyanin in concentrated hydrochloric acid, the solution on standing gradually loses its bright bluish-green colour and becomes of a dull olive-green. The solution now gives with water a brown precipitate, which filtered off and washed is almost entirely soluble in ether. The ethereal solution has a green colour with a tinge of red, and shows a spectrum consisting of eight bands ; it leaves on evaporation a semi-crystalline residue, which is green by transmitted, purple by reflected light. By the prolonged action of tin on a solution of phyllocyanin in hydrochloric acid a further and more complete change is effected, the solution acquiring a bright red colour without the least tinge of green[1]. On the addition of water the solution gives a red flocculent precipitate, which filtered off and washed dissolves in alcohol with a bright

[1] Berzelius observed a similar reaction on treating chlorophyll dissolved in hydrochloric acid with metallic zinc.

red colour; the solution turns lemon-yellow with caustic alkali, but the red colour is restored by an excess of hydrochloric acid; the solution leaves on evaporation a reddish-brown amorphous residue, which with ether gives a reddish-brown solution showing a peculiar and interesting spectrum of six bands. This red colouring matter, though derived from chlorophyll by a very simple process, does not in any way reveal its origin: it rather resembles some of the colouring matters of flowers.

The substance which is formed along with phyllocyanin by the action of hydrochloric acid on chlorophyll I call with Frémy phylloxanthin. Professor Stokes remarks that Frémy's phylloxanthin may differ according to the mode of preparation, and may be a mixture of several substances. This is no doubt possible, when Frémy's method, which consists in adding a mixture of ether and hydrochloric acid to an alcoholic extract of leaves, is adopted, for in this case the ether may contain colouring matters pre-existing in the leaf, and not necessarily related to chlorophyll, as well as products due to the action of acids on the latter. When Frémy[1] describes phylloxanthin as crystallising in reddish prisms like potassium bichromate, it is certain that what he saw was not phylloxanthin in the proper sense of the term; it was probably chrysophyll (erythrophyll), which has the appearance which he describes. Other observers—exhibiting a reprehensible want of accuracy in the use of terms—consider xanthophyll, the yellow colouring matter or mixture of colouring matters associated naturally with chlorophyll, and phylloxanthin to be synonymous; the two are, however, quite distinct; one occurs naturally, the other is a product of decomposition, and their properties are distinct. Let it be understood, then, that phylloxanthin is the product obtained by dissolving the precipitate formed by acids in an alcoholic extract of leaves in ether and adding concentrated hydrochloric acid to remove the phyllocyanin, when it remains dissolved in the upper ethereal liquid. This liquid, which has a dark greenish-yellow colour with a red

[1] Comptes Rendus, LXI. 190.

fluorescence, may still hold in solution some phyllocyanin along with phylloxanthin; the former is easily removed by shaking the solution with concentrated hydrochloric acid, this being repeated with fresh quantities of acid, until the latter takes up no more colour. The process must be conducted rapidly, because by prolonged contact of its solution with hydrochloric acid phylloxanthin undergoes a change which results in its becoming soluble in the acid, the latter even when quite colourless becoming blue on standing from the surface downwards, so as to make it seem as if under these circumstances phylloxanthin were really converted into phyllocyanin. After removal of the phyllocyanin, the phylloxanthin solution still contains a large quantity of another impurity, which I have so far been unable to remove. This impurity is the fatty matter, which is always deposited along with the colouring matters when hydrochloric acid gas is passed into a solution of crude chlorophyll, and which in the process adopted remains for the most part dissolved in the ether. When the ethereal solution is slowly evaporated it leaves a quantity of long pseudo-crystalline needles, sometimes accompanied by small crystalline rosettes which are brown by transmitted light; these consist of phylloxanthin, contaminated, however, with fatty matter. Solutions of phylloxanthin have a yellowish-green colour with a pronounced reddish tinge, and may be thereby distinguished from solutions of phyllocyanin which are more decidedly green. They show a spectrum of four bands only, that of phyllocyanin having five; an admixture of the latter with phylloxanthin may therefore be easily detected. The four bands which appear on the addition of a little hydrochloric acid to a solution of chlorophyll are due in my opinion to phylloxanthin, which is formed in the first instance; the appearance of a fifth band after the prolonged action of the acid indicates the presence of phyllocyanin. Whether phylloxanthin by the continued action of acid is converted into phyllocyanin, or whether the two colouring matters are formed independently, but in succession from chlorophyll, or whether lastly the two owe their formation to two distinct sub-

stances which together constitute ordinary chlorophyll, remains doubtful.

Some leaves, such as those of the dandelion, show, when immersed in dilute hydrochloric acid, very distinctly the successive formation of the two colouring matters. The leaves first turn greenish-yellow owing to the formation of phylloxanthin, but after some time this tint changes to a greenish-grey, indicating the presence of phyllocyanin. The hypochlorin of Pringsheim, as well as other derivatives of chlorophyll described by various observers as appearing in brown crystalline needles, are, I think, all phylloxanthin more or less pure. The nature of the change which chlorophyll undergoes by the action of acids is not known. In my opinion it is a chemical process, not a mere molecular one.

Action of Alkalis on Chlorophyll.

The action of alkalis on chlorophyll has been less frequently studied than that of acids, partly perhaps because alkalis do not produce such marked changes as acids do. When caustic potash is added to an alcoholic solution of chlorophyll the colour of the solution remains unchanged, and no alteration is observed in the spectrum. But when the alkaline solution is heated, a change in the spectrum takes place, which was first described by Chautard[1], who states that the band in the red, called by him 'bande spécifique,' is now found to have split into two, the addition of an excess of acid causing it to appear single again, the doubling re-appearing with alkali, and so on. The fainter bands of the chlorophyll-spectrum disappeared almost entirely in Chautard's experiment. Russell and Lapraik have also examined the effect produced by alkali on a solution of chlorophyll: they obtained in the first instance what they call a one-banded modification of chlorophyll, the single band of this modification dividing into two on the addition of a considerable excess of alkali. The chlorophyll-green of Hansen, obtained by treating chlorophyll with boiling

[1] Comptes Rendus, LXXVI. 570, 1273.

caustic soda lye, I have already alluded to. According to Tschirch, chlorophyll is converted by the action of alkali into what he calls chlorophyllinic acid ; Hansen's chlorophyll-green would then be the sodium salt of this acid. Tschirch, as well as Russell and Lapraik, state that after treatment with alkali chlorophyll becomes much more stable, both on exposure to light and on treatment with acids. This in itself would tend to prove that a chemical change has been induced by the alkali leading to the formation of a product, which we may call a modification of chlorophyll, if we choose. The experiments which I have made, and of which I shall now give a short account, render it all but certain that this is the case[1].

Fresh leaves—grass being the best material to use—are exhausted with boiling spirits of wine containing from 80–82 per cent. of alcohol. The green extract is filtered hot, and being allowed to stand for a day or two away from the light, yields a dark-green voluminous deposit, containing chlorophyll mixed with fatty and other matters. This deposit is filtered off for further treatment, the pale-green filtrate being rejected. The green mass on the filter is now to be treated with a boiling solution of soda in strong alcohol, which dissolves it in part. After standing some time the insoluble portion, consisting of fatty matter etc., is filtered off, and a current of hydrochloric acid gas is then passed through the dark-green filtrate until it acquires a strong acid reaction. The liquid first becomes yellowish-green, but after some time the colour changes to a dull purplish-green, and small crystalline needles, arranged in stars, purple by reflected and dull green by transmitted light, begin to appear on the sides of the glass, and continue to increase in quantity for some time. The crystalline substance thus obtained is filtered off, washed with alcohol, and purified by treatment with ether, which removes some fatty matter; it is then dissolved in a little chloroform, and this solution is mixed with several times its volume of absolute alcohol, when the substance is again deposited in long crystalline needles. Under the microscope these are seen to consist

[1] Proceedings of the Royal Society, XLIV. 448.

of acicular crystals, which are mostly opaque, but when very thin are transparent, and appear olive-coloured by transmitted light. In mass the substance appears of a fine purplish-blue colour, and shows a semi-metallic lustre. It is insoluble in water, sparingly soluble in alcohol and ether, more easily soluble in benzol and carbon disulphide, and very easily soluble in chloroform. The solutions when dilute have a dull purplish or pink colour, and show a peculiar and interesting absorption-spectrum, differing widely from that of other derivatives of chlorophyll, and characterised by the presence of a very dark band near the line *E*, followed by two paler ones, both however very distinct, nearer the blue end. By using methylic in place of ethylic alcohol in the extraction of leaves, and applying the same treatment as that just described, a compound differing slightly from that obtained by ethylic alcohol is procured; it crystallises in purple needles, which are more lustrous than those of the other compound; it is almost insoluble in alcohol and ether, but easily soluble in chloroform, the solution showing exactly the same absorption bands as that of the first compound. These compounds are the ethyl and methyl ethers respectively of a derivative of chlorophyll, the preparation and properties of which may now be shortly described.

The compounds are insoluble in aqueous alkalis, even on boiling, but they are immediately dissolved and decomposed on treatment with alcoholic potash or soda, the process being one of saponification. When the ethyl-compound is treated with boiling alcoholic soda it dissolves; the solution on standing deposits a sodium salt in the shape of a dark-green, almost black, semi-crystalline mass, which is filtered off, washed with absolute alcohol, and dissolved in water. The dark-green aqueous solution gives with acetic acid, of which a great excess must be avoided, a green flocculent precipitate, which is filtered off, thoroughly washed with water, and then dissolved in ether. On slow evaporation the ethereal solution yields regular, lustrous crystals of a substance which, I think, had never previously been described.

I have called this substance '*phyllotaonin*,' from its resembling in colour and lustre the eyes in the peacock's tail [1]. It may also be obtained by the action of caustic alkali on phyllocyanin, but in not nearly so pure a state as by the method just described. Hence it appears that by acting on chlorophyll, first with acid and then with alkali, the same product is finally arrived at, as by employing alkali in the first instance, and then acid, the ethers occupying only an intermediate stage in the latter process.

Phyllotaonin appears on evaporation of its ethereal solution in regular flattened crystals [2] or crystalline scales, which by reflected light appear of a fine peacock or steel-blue colour; the crystals are mostly opaque, but when very thin they are transparent and then appear brown by transmitted light. It melts at 184° C. to a brown resinous mass, with partial decomposition; heated on platinum it burns away without residue. It is insoluble in water, but easily soluble in alcohol and ether; the solutions have the same colour and show exactly the same absorption-bands as solutions of phyllocyanin; but if the least trace of acid be present in the solution the spectrum gradually changes in a manner to be presently described. It is soluble in benzol and carbon disulphide, and very easily soluble in chloroform, but insoluble in ligroin. From phyllocyanin, for which it might be mistaken, phyllotaonin may be easily distinguished by its dissolving in glacial acetic acid with a fine violet colour, the corresponding solution of phyllocyanin being of a dull green; it may also be distinguished by its behaviour to acids generally. In contact with acids phyllotaonin undergoes a series of changes, accompanied by corresponding changes in the absorption-spectrum. If to an ethereal or alcoholic solution of phyllotaonin a small

[1] *ταών*, a peacock.

[2] Dr. Burghardt, of the Owens College, describes the crystals as follows:—'Crystal system monosymmetrical, oblique, rectangular prism, formed by the combination of the ortho- and clino-pinacoids. . . . . They cleave parallel to the ortho-pinacoid distinctly. Examined in polarised light they exhibit depolarisation on rotating the Nicol's prism, the colour changing from a light-yellow to a rich brownish-red.

quantity of any acid be added, the colour of the solution changes slowly from green to brown, and now shows a peculiar and beautiful spectrum, characterised by two dark bands in the red and two pale but quite distinct bands in the green, bands I and IV *a* of the phyllocyanin or phyllotaonin-spectrum having apparently each split up into two (see Fig. 11 of the Plate). A further change takes place on standing, one of the bands in the green becoming darker, the other lighter. Here the action stops with dilute acids. In concentrated hydrochloric acid phyllotaonin dissolves, giving a bright bluish-green solution which contains the same product as that formed by the slow action of dilute acids. On treating phyllotaonin with boiling glacial acetic acid it dissolves, and the dark purple solution deposits on cooling crystalline needles of a fine purple colour, consisting doubtless of an acetate and showing in solution the same absorption spectrum as the ethyl and methyl compounds, which in other respects also they closely resemble. The products formed by the action of acids may in all cases be re-converted into phyllotaonin by means of an alkali. The process of re-conversion may be followed through its various stages with the crystallised acetate. If this be treated with aqueous potash in the cold it dissolves; acetic acid then gives a green precipitate which dissolves in ether, the solution showing the spectrum just described, but if boiling alcoholic potash be employed phyllotaonin is reproduced, as shown by the spectrum of the ethereal solution of the precipitate with acid. Under the influence of acetic acid the latter passes again through the series of changes previously described. That the changes, induced on the one hand by alkalis and on the other by acids, are due in the one case to hydration and in the other to dehydration, is exceedingly probable. It was the peculiar behaviour of phyllotaonin in presence of acids that led me to infer that it had never previously been observed.

Though there can be little doubt as to the crystallised substance formed by the action of acid on an alcoholic solution of alkaline chlorophyll being an ethyl compound, still

the attempts to reproduce the latter by the direct action of hydrochloric acid on an alcoholic solution of phyllotaonin failed. In order to explain its formation in the first instance we may suppose that by the action of alkalis chlorophyll is first converted into a substance—of which Hansen's chlorophyll-green is perhaps the sodium compound—which by decomposition with acids yields phyllotaonin, and this in the nascent state and in contact with alcohol and acid undergoes etherification. The purest specimen of the ethyl ether which I was able to obtain was found to contain in 100 parts

Carbon	66·49
Hydrogen	6·58
Nitrogen	3·32
Oxygen	23·61

To calculate a formula corresponding with these numbers would be premature; the small percentage of nitrogen—striking as compared with the amounts obtained in previous analyses of chlorophyll-derivatives—would render any such calculation uncertain.

There are few natural colouring matters or derivatives of the same, which, so far as my experience goes, surpass phyllotaonin and its compounds with regard to beauty and brilliancy of appearance combined with absorption-spectra of singular elegance to which no mere figures can do adequate justice.

Action of Aniline on Chlorophyll.

I was at first inclined to head this paragraph—action of aniline on green leaves. I have, however, arrived at the conclusion that the peculiar reaction which I am about to describe is due to chlorophyll, and not to any other constituent of leaves, though from its not taking place to the same extent with chlorophyll after removal of the colouring matter from the plant, I was at first inclined to believe that it might be due to some substance other than chlorophyll. The reaction is a very singular one, and may perhaps suggest new ideas regarding the nature and constitution of chlorophyll.

When fresh green leaves of almost any kind—the effect is best seen with young holly or beech leaves—are moistened as uniformly as possible with aniline by pouring the liquid over them, allowing to drain, pouring back, and so on, the leaves being left exposed to the air undergo a remarkable change. In a few minutes they generally begin to show dark spots of a brown colour, which gradually increase in size, until the green colour has at last entirely disappeared and given place to a uniform brown; with the leaves named the discoloration is completed in a few hours. The effect with green beech-leaves is to make them resemble those of the copper-coloured variety, while thicker leaves, such as those of the holly and ash, become dark brown, almost black, and nearly opaque. Now the chlorophyll of such anilised leaves, as they might be called, has almost entirely disappeared and been converted into another substance with totally different and very peculiar properties. In order to isolate this substance the leaves, after being exposed to the action of aniline for a day or two, are to be exhausted with boiling alcohol, which deprives them of the greater part of their colour, leaving them of a pale brown. The dark-brown extract, which shows some traces of chlorophyll absorption-bands, due to unmetamorphosed colouring matter, is evaporated or distilled down to a small volume, then mixed with water and sufficient hydrochloric acid to take up the excess of aniline, after which it is shaken up with ether. The latter dissolves nearly all the matter left behind by the acid and then appears brown. The ethereal solution after washing with water is filtered and evaporated slowly, when it leaves a brown crystalline residue. This is treated with a little cold alcohol which dissolves a portion with a dark-brown colour, leaving a residue, which being filtered off, washed with alcohol and dried, is treated with carbon disulphide. The latter dissolves nearly the whole, giving a solution of a deep yellowish-red, which filtered and evaporated spontaneously leaves plum- or chocolate-coloured silky needles mixed with some fatty matter. The latter may be removed by treatment with

boiling ligroin, in which the needles are nearly insoluble. This is the only well-defined product of the action of aniline on leaves; there may be others that are formed at the same time, but which cannot be separated from the fatty matters and other impurities accompanying them.

The discoloration of green leaves by aniline, which is due, in part at least if not entirely, to the formation of this product, takes place, I have found, with the leaves of the following plants:—common ash, buck-wheat, carrot, dock (*Rumex obtusifolius*), grass, groundsel (*Senecio*), hop, ivy, laburnum, lettuce, lime, yellow lupin, mignonette, mint, oak, pear, potato, privet, rhododendron, rue, also with the leaves of the following:—*Angelica*, *Antirrhinum*, *Azalea pontica*, *Calceolaria*, *Chrysanthemum*, *Dahlia*, *Geranium*, *Hypericum*, *Helichrysum*, *Lycium*, *Escholtzia californica*, *Spiraea*, *Pinus excelsa*, *Tropaeolum*, *Weigelia*; lastly with the fronds of the following ferns:—*Aspidium Filix-mas*, *Blechnum* sp., *Osmunda regalis*, and *Polystichum aculeatum*. This list is, I think, sufficiently extensive to justify the conclusion that the discoloration by aniline is a general property of green leaves. There are, however, some apparent exceptions to the rule. Among these cabbage leaves and the leaves of garden spinach and of *Rhododendron ponticum* may be named. These leaves, after being moistened with aniline and left exposed, remain green for a long time, and only very gradually acquire a brown tinge, many degrees less intense than that of most anilised leaves; they yield, however, on treatment a quantity of the same crystalline substance as other leaves do, though perhaps a little less than usual. The excess of aniline with which the leaves in these experiments have been treated and which is allowed to drain off, always contains a quantity of the crystalline substance in solution; on adding to it an excess of dilute hydrochloric acid a quantity of flocculent matter is left undissolved, from which some of the crystalline substance may easily be obtained.

That this process of decomposition or conversion by aniline affects the chlorophyll of the leaves chiefly is evident, for not

only is the colour of the leaves entirely changed, they also yield on treatment mere traces of chlorophyll or of ordinary decomposition products of chlorophyll, these having been almost entirely replaced by other products. Moreover, variegated leaves, for instance those of the white-leaved ivy, are only slightly tinged by aniline, and yield no trace of the crystalline product which green leaves afford. Some healthy green leaves from the Spanish chesnut, the tulip tree, and the common bindweed, treated together with aniline, became dark brown and yielded 0·044 grm. of the crystalline product, whereas the same quantity of leaves from the same plants, that had become yellow and fallen to the ground, turned light brown on treatment with aniline and yielded only 0·023 grm. of the same product; in the latter case it was evidently the residual chlorophyll of the faded leaves which reacted with the aniline. By immersion for some time in boiling water green leaves do not lose their property of becoming brown on being treated with aniline, but the colour is not so dark as in the case of leaves that have not been exposed to heat, and the crystalline product which they yield is somewhat diminished in quantity. With a knowledge of these facts one would hardly be prepared to find that chlorophyll after removal from the organs in which it was contained ceases entirely, or almost entirely, to react with aniline. A freshly prepared alcoholic extract of green leaves on the addition of aniline and evaporation at a gentle heat leaves a green syrup containing apparently unchanged chlorophyll, and after removal of the aniline by hydrochloric acid and water, the residue remaining undissolved, contains the ordinary decomposition products of chlorophyll with acids, generally without a trace of the peculiar product due to aniline. In one case—using an alcoholic extract of grass—I did obtain a small quantity of the product after addition of aniline and evaporation, but after being kept for some time in a stoppered bottle, the extract—a part of which only had been used—lost the property of reacting with aniline without being at all changed in other respects. It appears therefore that the aniline-reaction manifests itself strongly and

almost immediately with chlorophyll while still lodged in the vegetable cell; very soon ceasing to appear, and being generally not even perceptible with ordinary chlorophyll in solution. The explanation of this singular fact might possibly present no difficulty to the physiologist, who would perhaps say that the one is physiological, living chlorophyll, the other chemical, dead chlorophyll,—a view which it would be difficult to controvert, except by restoring to ordinary chlorophyll, by a chemical process, the property which it possessed while forming part of the living organism, and which it lost in consequence of the treatment employed for the purpose of extracting the colouring matter. Be this as it may, it is certain that this anilising process, as it may be called, ends in the formation of a definite, crystallised chemical substance, the properties of which are no less peculiar than is its mode of formation. I propose to call this substance *anilophyll*, a name which simply points to its origin without involving anything hypothetical.

Properties of anilophyll. When prepared in the manner above described it consists of lustrous needles, which in the mass appear garnet-red with a tinge of purple, and by transmitted light are light brown. It melts at 190–192° C.—the determination having been made with five specimens prepared at various times—to a dark brown liquid, and being heated more strongly burns easily without leaving any residue. It dissolves, but not very readily, in boiling ether; the solution is yellow and resembles a watery solution of isatin; it shows no absorption-bands in any part of the spectrum, and no absorption in the red and yellow, but a good deal in the green, and still more in the blue. It is more soluble in boiling alcohol than in ether, giving an orange-coloured solution, which on cooling deposits fine silky needles arranged in rosettes and fan-shaped masses, the liquid becoming nearly colourless. It is easily soluble in chloroform and carbon disulphide as well as in boiling glacial acetic acid, but is only slightly soluble in boiling ligroin. The colour of the solutions when concentrated resembles that of ferric sulphocyanide,

but is yellower at the edges; they show no absorption-bands. Anilophyll is slightly soluble in boiling concentrated hydrochloric acid, giving a solution of a fine violet colour without absorption-bands. It dissolves easily in concentrated sulphuric acid in the cold, giving a dark-red solution which on the addition of more acid shows about the same colour and the same amount of absorption as the ethereal solution; on the addition of water the solution gives no precipitate and remains red, but after some time it acquires a fine violet colour like that of an alkaline solution of alizarin, and now shows a broad ill-defined absorption-band in the orange, with much obscuration in the green, but very little in the blue and none in the red. On raising the solution in sulphuric acid to the boiling-point and boiling some time no decomposition seems to take place, the solution remaining red and giving as before no precipitate with water. On treatment with strong nitric acid, anilophyll dissolves affording a bright red solution, which on boiling gives off only a trace of nitrous fumes, and on evaporation leaves an amorphous, red, resin-like residue, which is probably a nitro-compound, since it differs in some respects from the original substance. Anilophyll is totally insoluble in caustic alkalis, the crystals remain quite unchanged on boiling and the liquid acquires no trace of colour; the addition of zinc powder to the boiling lye is quite without effect, no sign of reduction or of consequent solution being observable. On treating anilophyll with fusing potassium hydroxide and continuing to heat for some time, no apparent change occurs, the residue left after washing away the excess of alkali being insoluble in water. The substance is however not quite the same as it was, for after treatment with the melting alkali it has become easily soluble in alcohol, giving a bright red solution, which on evaporation leaves an amorphous red residue with a slight golden lustre; the solution shows no absorption-bands.

It appears therefore that, by the action of aniline on chlorophyll, more especially the chlorophyll of living plants, a substance is formed which no longer shows, even in a modified

state, any of the characteristics of chlorophyll. Its colour is entirely different; its solutions show no trace of absorption-bands, the total absence of which is seen in the case of no other derivative of chlorophyll; it is an exceedingly stable body, more so than any other colouring matter or derivative of a colouring matter that I am acquainted with; it reveals in fact no sign or trace of the source whence it was derived. And yet the process whereby it is formed cannot be a destructive or a complicated one. A green leaf exposed to the vapour of aniline at the ordinary temperature becomes brown almost as rapidly as a red rose changes to green in an atmosphere charged with ammonia; the organic structure of the leaf, moreover, is not in the least affected. The process is so strange and so entirely, I imagine, without analogy as to suggest doubts whether it is really living chlorophyll, as I call it, and not rather something else that is concerned in the formation of anilophyll; but after much consideration of the facts I have found it impossible to arrive at any other conclusion than the one I have given.

That anilophyll probably belongs to the well-known class of compounds called anilides is a supposition that would naturally occur to any one conversant with modern organic chemistry. If so it should like other anilides be decomposed by strong acids and alkalis, reproducing the substance from which it was originally formed; we should expect it to yield, if not chlorophyll, at least some derivative of the latter, such as phyllocyanin. It is capable, however, of resisting the action of the strongest acids and alkalis to a remarkable degree, as I have stated. In no other derivative of chlorophyll are the original characteristics of the latter so completely masked or obliterated as in this.

That something besides aniline concurs in the formation of anilophyll seemed probable from the fact that when green leaves are entirely immersed in aniline they remain green, and only become brown in the way described on being taken out and exposed to the air. Hence it would naturally be inferred that the element required to complete the reaction is oxygen.

This conclusion seemed to be confirmed by an experiment made in an atmosphere of hydrogen gas. One pound of green ivy leaves and the same weight of holly leaves were each placed loosely packed in a large flask, into which well-washed hydrogen gas was passed for several hours. The flasks being left to stand over night, hydrogen was again passed in, so as to remove any gas that might have diffused out of the leaves. A small quantity of aniline was then introduced into each flask and the leaves were moistened as uniformly as possible with the liquid, after which they were left to stand well covered for a day or two. In neither case was the least change of colour apparent in the leaves. When treated with boiling alcohol they afforded extracts of the usual chlorophyll-green colour, and these extracts, when examined in the manner before described, yielded no trace of anilophyll. Nevertheless, the conclusion to which this experiment would naturally lead, that it was the absence of oxygen that was the cause of the negative result in this case, was rendered uncertain by the next experiment, in which leaves of the same kinds were taken, the hydrogen being however replaced by carbonic acid gas. Here the leaves after contact with aniline turned brown as rapidly as in air, and the amount of anilophyll obtained seemed to be the same as usual. It would appear therefore that it is rather carbonic acid than oxygen that is required in this process, and that in the experiment with hydrogen it was the removal by diffusion of the carbonic acid present in the leaves that led to the negative result obtained. The experiments are, however, too few to justify very positive conclusions. I hope to resume them at a more favourable season when a greater variety of material to work upon will be available [1].

[1] I venture to express the wish that others who may be working at the chemistry of chlorophyll will allow me a little time to continue undisturbed my experiments on this part of the subject. The reaction above described was only discovered in the summer of 1888, and before I had advanced very far in its study the green foliage of the season had faded. I intend, health permitting, to continue my experiments in the approaching spring.

Substances accompanying Chlorophyll.

An account of the substances accompanying chlorophyll might include all the contents of the leaf-cell. I shall here, however, exclude all such substances as are soluble in water and confine myself to the yellow colouring matters of leaves soluble in alcohol and ether, but insoluble in water. These substances usually accompany chlorophyll in ordinary alcoholic or ethereal extracts of green leaves, and having some properties in common with chlorophyll have been supposed, though perhaps without sufficient reason, to be related to it. According to the definition of chlorophyll occasionally given it would include all the green and yellow colouring matters of ordinary leaves. The earlier observers did not indeed recognise the simultaneous presence of yellow and green pigments in ordinary green leaves. Berzelius[1] supposed that the yellow colouring matter of autumnal leaves was formed from chlorophyll in consequence of a change in the organisation of the leaf induced by cold, and he called it xanthophyll. Krauss endeavoured to show that ordinary chlorophyll is a mixture of two colouring matters—kyanophyll and xanthophyll, the latter being the substance to which the obscure bands at the blue end of the spectrum of ordinary chlorophyll-solutions are mainly due. In this case there has fortunately been no misuse of terms, there being good reasons to suppose that the xanthophyll of autumnal leaves is merely the yellow colouring matter left after the fading away of the green, the latter being the less stable of the two and disappearing first. Still the term xanthophyll, if applied to the yellow pigment of etiolated leaves, to the yellow colouring matter accompanying the chlorophyll of green leaves, and to that of yellow autumnal ones, granting that these three are virtually the same, may after all denote not one, but a group of substances having similar properties. As regards the xanthophyll of green leaves this is exceedingly probable. Tschirch, after

[1] Ann. d. Pharm. XXI. 261.

an able summary of what is known on this subject, arrives at the conclusion that there are five distinct xanthophylls, not including the etiolin of etiolated leaves, which according to him differs more widely from the xanthophylls than do the latter *inter se*. I have myself ascertained that the xanthophyll of faded leaves does consist of at least two distinct colouring matters, one of which is soluble in alcohol and ether, the other soluble in alcohol only; the first shows the same absorption-bands as the erythrophyll of green leaves, the latter no bands at all. Much confusion has arisen in connexion with this subject in consequence of the difficulty of separating these colouring matters and of ascertaining what bands belong specially to each, spectroscopic observation being the only means hitherto employed to distinguish them. Some observers maintain that the bands seen at the red end in the absorption-spectrum of most of the yellow colouring matters belong to them, while others are of opinion that these bands are due to an admixture of chlorophyll or some derivative of chlorophyll, e.g. phyllocyanin, of which a small quantity not otherwise discoverable would suffice to produce the absorption, and that, if these xanthophylls could be obtained in a state of purity, they would no longer when dissolved show any bands at the less refrangible end of the spectrum. The latter opinion certainly holds good as regards chrysophyll, the only one of the yellow colouring matters of leaves that has hitherto been obtained in a state of purity. When leaves of any kind are extracted with boiling alcohol the extract on standing for some time invariably deposits a quantity of minute sparkling red crystals, almost always mixed with more or less fatty matter coloured green by chlorophyll. These crystals are the chrysophyll of Harsten, the erythrophyll[1] of Bougarel. The substance may easily be obtained in a state of purity by treating the deposit referred to with a little chloroform, filtering, adding alcohol to the filtrate, collecting the crystals which form on standing,

[1] The erythrophyll of Berzelius is the substance to which the colour of red autumnal leaves is due, and in no way resembles the colouring matter of Bougarel.

and repeating the process with chloroform and alcohol so as to free the substance entirely from adhering fatty matter. The crystals are very regular in shape, of a deep orange or red colour by transmitted light with a golden lustre by reflected light. This beautiful and interesting substance, the properties of which have been studied by Bougarel and others, yields solutions of a golden-yellow colour which, when sufficiently dilute, show two tolerably well-defined bands, one on the line *F*, the other between *F* and *G*, whilst at the red end of the spectrum not a trace of an absorption band can be seen, however strong the solution may be, though the band between *B* and *C* does appear when the solution is not quite pure, i.e. when it still contains traces of chlorophyll or of chlorophyll-derivatives. Hence it appears probable that the other xanthophylls, if they could be isolated and obtained in a state of purity, would like this one show no bands at the red end of the spectrum. On the other hand, the bands seen at the blue end probably do not belong to chlorophyll, strictly speaking, but to one of the xanthophylls. The bands of chrysophyll do not, however, as might have been supposed, exactly coincide with those at the blue end of the ordinary chlorophyll-spectrum, being a little nearer the red end. Tschirch surmises that chrysophyll does not pre-exist in the green leaf, but is formed by the action of acids either from chlorophyll itself or from one of the xanthophylls accompanying it. If this be the case it would account for the non-appearance of the chrysophyll-bands in ordinary extracts of green leaves. Solutions of chrysophyll are bleached on exposure to air and sunlight almost as easily as are those of chlorophyll; still its presence may be detected, if spectroscopic observation only may be relied on, in the yellow alcoholic extracts of faded leaves[1].

It is perhaps one of the xanthophylls to which is due the glucose reaction observed by myself[2] several years ago after

[1] According to Arnaud (Compt. Rend. CII. 1119, and CIV. 1293), chrysophyll is identical with carotin, the yellow colouring matter of carrots.

[2] Proceedings of Roy. Soc. XXXVI. 183.

treating ordinary chlorophyll-solutions with acids, since the substance is to a great extent removed by agitating the solution—in accordance with the suggestion of Professor Stokes—with carbon disulphide, being afterwards found in the lower yellow liquid. R. Sachsse[1] claims to have first discovered and prepared the glucoside accompanying chlorophyll, to which this reaction is due.

Chlorophyll in Animals.

The question as to the existence of chlorophyll in animals has been much debated. It would indeed seem *à priori* improbable, considering what the functions of chlorophyll are, or are supposed to be, that it should be found in the organs of any true animal. In some cases, as in that of *Bonellia viridis*, the colour is not due to chlorophyll, as had at one time been supposed, but to a substance of similar properties, to which the name *Conellein* has been given. In other cases the formation of chlorophyll is due to parasitic algæ existing within the animal organism, and is therefore not the direct product of the latter. There are some cases, however, where it is present in and formed by the animal itself, as shown by Professor Ray Lankester, who found that the green colour of *Spongilla fluviatilis* and *Hydra viridis* was due to chlorophyll present in the cells, and not to parasitic algae. Dr. MacMunn has found a chlorophyll in the digestive glands (so called 'livers') of various invertebrate animals[2], which gives a spectrum and reactions similar to those of plant-chlorophyll, the term chlorophyll being here used in the wider sense. This pigment he named entero-chlorophyll. He also found a chlorophyll in several sea-water sponges[3], and verified the statement of Pocklington—called in question by Krukenberg and Chautard—that chlorophyll is present in the elytra of cantharides beetles[4]. With regard to the function of animal chlorophyll, Dr. MacMunn suggests that it is probably respiratory.

[1] Chem. Centralbl, Feb. 1884.
[2] Proceedings of Roy. Soc. XXXV. 370.
[3] Journ. Physiol. IX. 1.
[4] Brit. Assoc. Rep. 1883.

My object in referring here to the subject of chlorophyll in animals is to impress on physiologists the desirability of not resting satisfied with a mere superficial examination of any colouring matter supposed to be chlorophyll. In order to be decisive the requisite experiments need not be many, nor do they require a great amount of material to work on. In doubtful cases I would recommend the following method:—A moderately strong solution of the colouring matter having been obtained, compare its absorption-spectrum with that of chlorophyll. After the addition of a few drops of hydrochloric acid to some of the solution contained in a test tube, compare the spectrum, if changed, with that of acidified chlorophyll. Then add some acid to a larger quantity of the solution, and allow to stand for several days; filter off the dark-coloured deposit which will have formed—provided chlorophyll was present and the solution was sufficiently strong—and dissolve some of it in ether, then compare the spectrum of the solution with that of phyllocyanin (Fig. 4 of Plate). Dissolve the rest of the deposit or part of it in hot alkaline lye, add an excess of acetic acid, shake up with ether so as to dissolve the flocculent precipitate, and allow to stand for several days, after which the solution should show the peculiar spectrum of the substance produced by the action first of alkali and then of acid on phyllocyanin (see Fig. 11 of Plate). If these four spectra are distinctly seen and identified, the colouring matter under examination is certainly chlorophyll.

Chemical Constitution and Functions of Chlorophyll.

Considering the present defective state of our knowledge of chlorophyll as a chemical individual, considering how little we actually know of its properties and composition, it may appear somewhat premature to indulge in speculations as to its constitution and functions,—but to one who has worked long at the subject the temptation to do so is almost irresistible. Without entering on the question of the functions of chloro-

phyll, as connected with its properties in general, I will simply record some thoughts and suggestions that have occurred to me relative to the purely chemical side of the question, putting entirely on one side all that relates to the purely physical properties of chlorophyll, to its colour for instance, and its consequent power of absorbing heat and light in a peculiar manner, properties which, though undoubtedly important, can only be profitably studied by the physicist. My remarks, possibly in themselves of little importance, may perhaps serve to stimulate further inquiry.

In removing chlorophyll from the class of resins, where it had previously been placed, to that of colouring matters, Pelletier and Caventou undoubtedly took a step in advance; using the phraseology of modern chemistry, they placed it in the aromatic series of carbon compounds. No general views of importance regarding the constitution of chlorophyll are met with before the time of Hoppe-Seyler, who thought that his chlorophyllan might be a substance belonging to the lecithin class, yielding like other lecithins glycerine-phosphoric acid and choline as products of decomposition, and in addition to these chlorophyllanic, and perhaps fatty acids. In what relation chlorophyllan stands to chlorophyll itself he does not state. Tschirch thought that chlorophyllan itself was a product of oxidation of chlorophyll, into which it might be reconverted by the reducing action of zinc powder, but whether the chlorophyll so regenerated was identical with the natural colouring matter seems doubtful, Tschirch himself admitting that they differ in some respects. The lively green colour of the solutions of the compounds obtained in the manner I have described by bringing phyllocyanin, organic acids, and various metallic oxides together, a colour very nearly resembling that of true chlorophyll-solutions is so striking that, taken together with the resemblance between the absorption-spectra of some of these solutions and that of chlorophyll, one is almost led to suppose that chlorophyll had in some cases been actually reproduced from phyllocyanin. This is indeed true in a certain sense, I think, i.e. in every case, whatever acid or whatever

base has been employed, a kind of chlorophyll is obtained, though not the natural chlorophyll of plants. In order to explain what I mean, I will assume, as Hoppe-Seyler does with regard to his chlorophyllan, that chlorophyll is a kind of lecithin, of which phyllocyanin forms as it were the nucleus. Its composition may be roughly represented by the formula

$$x \text{ phyllocyanin} . x\,y,$$

in which x represents an unknown acid, or it may be more than one acid—e.g. phosphoric acid and margaric acid—y an unknown base, it may be choline, the constituents or their residues being linked together to form a complex, such as is frequently met with in substances of organic origin. Now when this complex is acted on by an acid it is more or less rapidly decomposed; if hydrochloric acid be used the final result is the formation of phyllocyanin hydrochloride, which in presence of much water is decomposed, leaving free phyllocyanin, and of the hydrochloride of the unknown base, while the acid x is set at liberty. If x be a fatty acid, and the solution be an alcoholic one, it is possible that some of the acid may be deposited along with the phyllocyanin, and that a portion of the fatty matter, which is always found mixed with the deposited phyllocyanin, may be due to the decomposition of the chlorophyll by acid. When caustic alkali acts on chlorophyll, the base y is removed, potassium, sodium, or ammonium entering into the complex, though the action is not so simple as in the case of acids, since the phyllocyanin also undergoes some change by the action of alkali, as I have already explained. In contact with aniline, chlorophyll yields up the base y, which is simply replaced by aniline forming anilophyll, which may be called a substituted chlorophyll, though why in this case there should be such a complete metamorphosis is difficult to understand [1].

In the case of the artificial chlorophylls, as they may be called, the factors x and y are known. Tschirch's regenerated chlorophyll is in my opinion a chlorophyll which con-

[1] In the above hypothetical formula phylloxanthin may be put in the place of phyllocyanin.

tains zinc and some kind of fatty acid. The various phyllocyanin compounds which I have described are chlorophylls which contain either zinc, iron, copper, or silver, and an acid, which may be either an organic acid or phosphoric, or even exceptionally carbonic acid. Of these compounds the cupric ones approach anilophyll in stability, while the zinc compounds, as before mentioned, closely resemble natural chlorophyll in more than one respect. If the properties of the ferrous compounds corresponded more nearly with those of natural chlorophyll, it would be permissible to suppose that the latter is an iron compound, for though the percentage of ferric oxide in the ash of chlorophyll is but small, the amount might perhaps suffice to form a saturated compound with phyllocyanin, the atomic weight of which is probably very high. The properties of the ferrous compounds, however, differ too widely from those of chlorophyll to allow of this supposition. The only probable conclusion therefore is, that the factor y in the formula of natural chlorophyll represents an organic base, perhaps choline, as suggested by Hoppe-Seyler. Were this base known there would be some hope of our being able to build up a compound which should be identical with natural chlorophyll.

I venture in conclusion to bring forward one more hypothesis; it is this, that the factor x in the chlorophyll formula may represent carbonic acid. A weak acid like carbonic acid would form with phyllocyanin, itself a weak base, and the unknown base y, also perhaps weak, a compound the proximate constituents of which would probably not be very firmly united, and which would therefore easily split up when exposed to any disturbing influence. It is possible that the first stage of the decomposition of chlorophyll—the one which it undergoes by the action of heat alone or of very weak acids—may consist simply in the elimination of CO_2, and that it is this loss which renders it incapable after being kept in solution for some time of forming anilophyll on being brought into contact with aniline. It may be too the removal of the loosely combined CO_2 after leaves have been

kept for some time in hydrogen gas that caused the negative result on subsequent treatment with aniline in the experiment above described. If CO_2 be, as I suppose, essential to the constitution of chlorophyll it must be equally so to that of anilophyll, which is from my point of view simply a substitution product of unaltered chlorophyll. If this be the constitution of chlorophyll it will be readily conceived how difficult it would be to reconstruct the natural substance by artificial means, for a mere knowledge of its proximate constituents, all of them endowed with weak affinities, would constitute merely the first step towards the accomplishment of the task.

The presence of a body having a chemical constitution such as I attribute to chlorophyll would, it is evident, serve a useful purpose in the vegetable economy. The carbonic acid forming one of its constituents being held more loosely combined than in an ordinary carbonate, and yet in a state of greater condensation than it would be in a mere watery solution, would be in a favourable condition for transfer to the assimilating plasma which effects its decomposition with elimination of oxygen, and the chlorophyll would then be in a state to take up fresh quantities of CO_2, acting therefore as a carrier of carbonic acid in the plant, just as haemoglobin serves to convey oxygen in the animal economy.

EXPLANATION OF FIGURES IN PLATE VII.

Illustrating Dr. Schunck's paper on the Chemistry of Chlorophyll.

Absorption Spectra of Chlorophyll and of some of its Derivatives.

Fig. 1. Chlorophyll in alcohol.

Fig. 2. The same very much diluted so as to show the bands at the blue end of the spectrum (by sunlight).

Fig. 3. Chrysophyll (erythrophyll) in ether (by sunlight).

Fig. 4. Phyllocyanin in ether.

Fig. 5. Phyllocyanin in concentrated hydrochloric acid.

Fig. 6. Phylloxanthin in ether.

Fig. 7. Phyllocyanin cupric acetate in alcohol.

Fig. 8. Phyllocyanin ferrous palmitate in alcohol.

Fig. 9. The same after treatment with cold hydrochloric acid.

Fig. 10. Phyllocyanin zinc carbonate in alcohol.

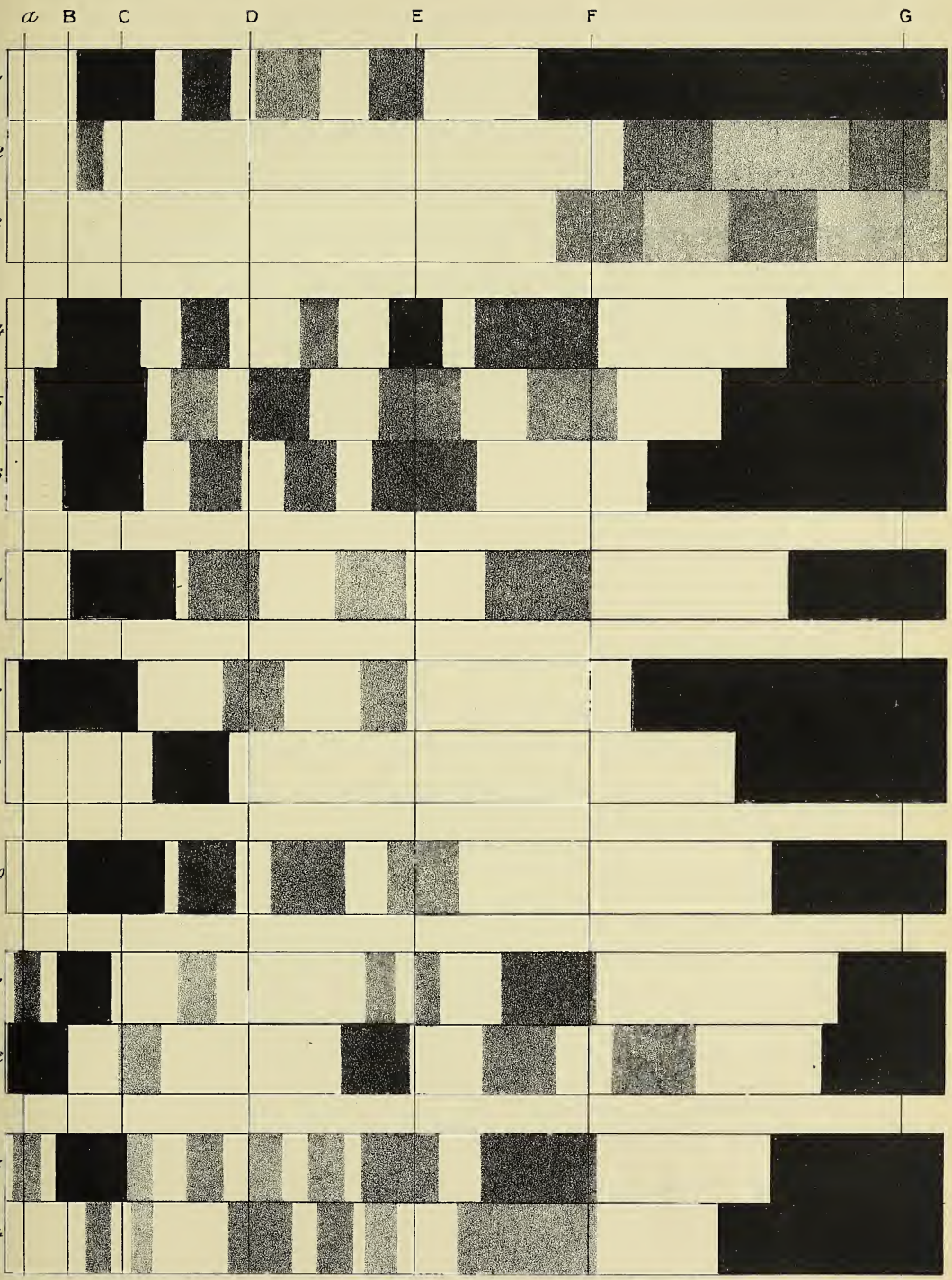
Fig. 11. Product obtained by treating phyllocyanin with caustic alkali, then with acid, or by treating phyllotaonin with acid, in ether.

Fig. 12. Ethyl-phyllotaonin, in ether.

Fig. 13. First product of the action of tin and hydrochloric acid on phyllocyanin, in ether.

Fig. 14. Final product of the action of tin and hydrochloric acid on phyllocyanin, in ether.

NOTE.—The spectra represented on this plate were observed and drawn by my son, Charles A. Schunck.—E. S.



C A. Schunck del.

University Press, Oxford.

SCHUNCK. — ON CHLOROPHYLL.

NOTES.

PRELIMINARY NOTE ON THE DISTRIBUTION AND STRUCTURE OF WATER-PORES (STOMATA) ON COTYLEDONS.—During the past summer (1888), while examining the histological structure of *Campanula rapunculoides* in the Laboratory at the Royal Botanic Garden, Edinburgh, I found that the stomata of the cotyledons were arranged in a peculiar manner; and this led me to investigate the cotyledons of a number of seedlings then growing in the Gardens.

The following is an abstract of these investigations :—

CAMPANULA RAPUNCULOIDES (Fig. 1).—In the cotyledon of *Campa-*

Fig. 1. Group of water-pores on upper epidermis at apex of cotyledon of *Campanula rapunculoides*. Triangular patch at apex shows water-pores and very small epidermal cells with straight or curved walls. No stomata occur on any other part of the upper surface. The other epidermal cells are large, and vary in outline.

nula rapunculoides the median vein forks before reaching the apex; the two branches of the fork form the sides, and the slightly concave apex the base, of a triangular patch. Water-pores occur among the epidermal cells on the upper surface of this patch, and resemble ordinary stomata, except that they are smaller. The epidermal cells of this patch are also smaller and less wavy in outline than the other epidermal cells of the plant. No pores or stomata occur anywhere else on the upper epidermis.

On the under surface of the cotyledon the arrangement is the opposite of that on the upper: the whole surface, except the triangular apical patch, is well supplied with stomata; the cells of the triangular patch are small and rectangular, but have neither pores nor stomata. The epidermal cells under the median vein are long and rectangular, and have no stomata.

Under the triangular patch of cells the median vein anastomoses with two lateral secondary veins which previously branch off from the median; these veins lose their spiral vessels and the prosenchyma alone forms a broad epithem which occupies the space under the triangular patch.

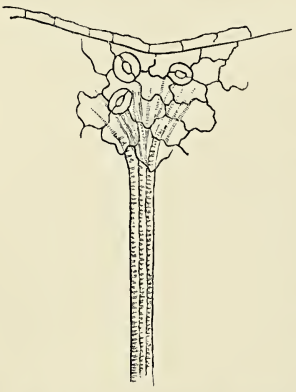


Fig. 1 *b*. *Campanula rotundifolia*. Group of three water-pores at apex on upper surface of cotyledon. The median vein of spiral vessels terminates in prosenchyma under the pores. Six or seven ordinary stomata occur on the rest of the surface.

The cotyledons of *Campanula rotundifolia, C. pyramidalis, and C. persicifolia* resemble those of *C. rapunculoides*.

C. rotundifolia (Fig. 1 *b*) has fewer water-pores—only three or four—but in addition it has six or seven stomata among the epidermal cells of the upper surface. The whole of the under surface is supplied with normal stomata, and the apex differs from the rest of the under surface only in having smaller cells.

The upper surface of the cotyledons of *C. pyramidalis* resembles that of *C. rapunculoides*; the under surface that of *C. rotundifolia*.

The cotyledons of *C. persicifolia* resemble those of *C. rapunculoides*, but the water-pores are only six or seven in number.

Collinsia grandiflora (Figs. 2, 2 *a*).—On the upper surface, near the apex of the cotyledons, are one or two water-pores which lead down into a large chamber. The guard cells of these pores, as well as the epidermal cells around them, often break down and leave a

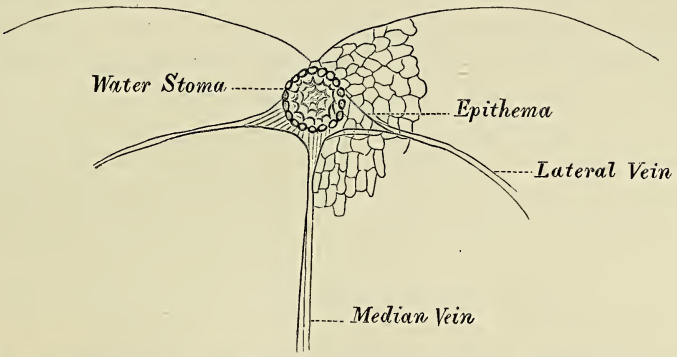


Fig. 2. Water-pores over epithem on upper epidermis at end of median vein in cotyledon of *Collinsia grandiflora.*

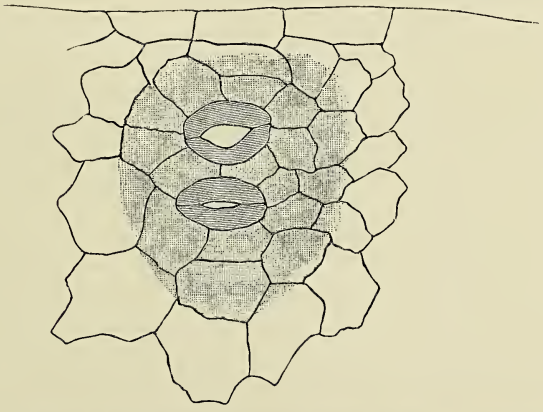


Fig. 2 *a*. *Collinsia grandiflora.* Apex of upper surface of cotyledon showing two water-pores.

cup-shaped depression near the apex of the upper epidermis. If a longitudinal section is made through this chamber and part of the median vein, the spiral vessels are seen to end immediately before the chamber is reached, but the prosenchyma of the vein runs forwards and upwards around the chamber.

There are no stomata on the upper epidermis, and the cells of the latter have straight or slightly curved walls, while many of them are developed into small blunt papillae.

The under epidermis has cells with wavy outlines and many stomata.

Utrica pilulifera (Fig. 3).—The cotyledon has a deep apical sinus, at the base of which is a multicellular knob-like gland. Behind this

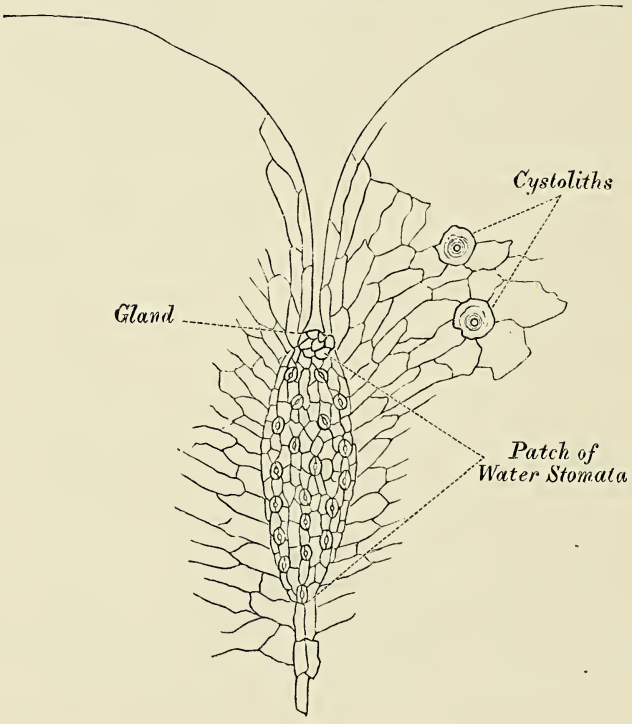


Fig. 3. Group of water-pores on upper epidermis at apex of cotyledon of *Urtica pilulifera*. Observe the gland at base of the apical sinus; the patch of water-pores behind the gland; and the cystoliths. No other stomata occur on the upper epidermis of the cotyledon.

gland is the apical patch of water-pores, which are more numerous —fifty or sixty—than in *C. rapunculoides*.

The epidermal cells of the upper surface are slightly curved or rectangular. There are no stomata, but a surface view shows special rounded cells—the cystolith-cells.

The under epidermal cells are of the usual wavy type with many stomata.

Polemonium caeruleum.—The cotyledons of *Polemonium caeruleum* have stomata on their upper surfaces, except over the apical patch, which is also destitute of water-pores. The epidermal cells and stomata of the under surface are of the usual type. Near the apex of the under surface are five or six water-pores. This plant, therefore, forms an exception to the foregoing types in having its water-pores on the under surface.

Convolvulus major (Figs. 4, 5).—The cotyledon is bilobed in *Convolvulus major*. Ordinary stomata are found on the under; much fewer on the upper surface. The median vein branches dichotomously

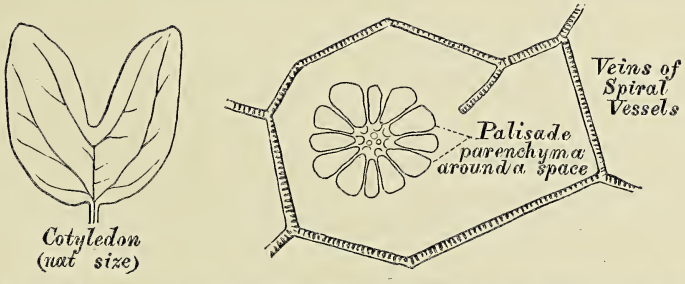


Fig. 4. Cotyledons of *Convolvulus major*, showing regular intercellular spaces among the palisade parenchyma. Large regular intercellular spaces, surrounded by palisade parenchyma, appear in polygonal areas near the apex of the cotyledon. Spiral vessels form the boundaries of the areas.

before reaching the base of the apical sinus, and sends a branch into each of the lobes. Between the base of the sinus and the forking of the vein is a triangular area which is divided into a number of polygonal spaces by means of a network of spiral vessels. In the middle of each space is a cavity which displaces, and is surrounded by, palisade parenchyma. Some of these cavities are separated from the upper epidermis by a single layer of palisade parenchyma; others have no palisade-cells between them and the upper epidermis; but none have been observed to open through the epidermis. A spiral vein has been indicated, in the horizontal section, passing from the polygonal boundary of one of these areas towards the cavity; and the ending of a spiral vein is seen in one of the cavities in vertical section. Each of these cavities seems to be an epithem, but no true stoma has been observed leading from the cavity.

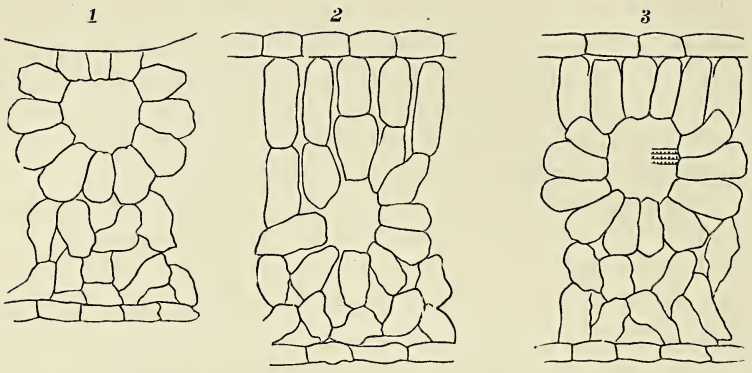


Fig. 5. Cotyledons of *Convolvulus major*. Transverse sections through intercellular spaces. Observe the varying depth of the space in the palisade parenchyma. Over (1) the epidermis has disappeared, and the palisade cells have become shortened, thus bringing the space near the surface. (3) Shows termination of spiral vessels.

Many cotyledons which have no apical group of water-pores have scattered stomata over their upper surfaces, in addition to the usual stomata of their under surfaces. The following plants show these characters:—*Iberis amari*, *Saponaria calabria*, *Agrimonia Eupatoria*, *Calendula officinalis*, *Rhodanthe Manglesii*, *Centaurea americana*, *Convolvulus minor*, *Anagallis arvensis*, and *Kaulfussia amelloides*.

The grouping of stomata and water-pores in cotyledons does not seem to have been previously investigated, except in the case of one or two plants. Kerner, whose 'Pflanzenleben[1]' has been published during the present year, says: 'Those cotyledons which have expanded and become green, display all the characteristics of foliage leaves: the epidermis is furnished with stomata.' Gravis, who has published an exhaustive Monograph on *Urtica dioica*[2], describes the gland and group of water-pores at the apex of the cotyledon; these are similar to the gland and water-pores of *Urtica pilulifera* of the present paper. In a foot-note Gravis refers to a similar group discovered by C. E. Bertrand, in the cotyledons of *Gunnera*.

No general conclusions, regarding the water-pores of cotyledons, can be drawn until many more types have been examined. The

[1] P. 582, vol. i, Pflanzenleben, by Anton Kerner von Marilann. Leipzig, 1888.
[2] Recherches Anatomiques sur les organs végétatifs de l'*Urtica dioica* (L.), par A. Gravis. Bruxelles, 1885.

stomata of cotyledons do not seem to vary much on the under surface; but on the upper surface there is greater difference. Water-pores, when present, are usually found on the upper epidermis over the epithem, which is formed at the end of the median vein. When water-pores are present there are few or no stomata on the upper epidermis, when absent there are many stomata.

This would lead one to suppose that a group of a few water-pores at the apex of a cotyledon is equivalent to many scattered stomata which appear over the upper epidermis in the absence of water-pores; but no weight can be attached to this until the subject has been more fully investigated.

ROBERT TURNBULL, Edinburgh.

A DISCOVERY IN CONNECTION WITH THE PRODUCTION OF HYBRID FERNS.—Occasionally in a batch of seedling ferns there will occur several plants of some strange marked variety identical in their characters, and I have long suspected that these were produced on one and the same prothallus; indeed this seemed evident in four instances of remarkable seedling Athyriums, yet the development was too far advanced to enable me to be absolutely certain. However, in order to prove this a number of Scolopendriums were planted in the prothallus state, and on the young fronds appearing a few days ago, two separate fronds were noticed identical in character and unusual in form, which, when examined by the aid of a magnifying glass, were found to have their origin in one well-developed prothallus. With a penknife it was possible to divide the prothallus so as to secure two plants, and this was not the only instance observed. Next season's growth will prove whether these plants will retain their likeness to each other.

E. J. LOWE, Shirenewton Hall.

FURTHER NOTE ON SPONGOCLADIA.—With reference to our paper on *Spongocladia* in Annals of Botany, Vol. II, p. 169, we wish to make public a suggestion, kindly made by Dr. Hauck in a letter, that the supposed symbiotic relationship between sponge and

alga gains in probability by the observations of Dr. Marchesetti on a floridean alga (*Marchesettia spongioides*, Hauck). The alga is described and figured by Dr. Hauck in the Atti del Museo Civico di Storia Naturale di Trieste, vol. vii, p. 236, Tab. 3, and Dr. Marchesetti's paper, *Sur un nuovo caso di Simbiosi*, is at p. 239 of the same volume. The alga in this case is, as has been said, floridean (*Areschougiaceae*), is sponge-like in appearance, and is furnished with 'oscula.' Small masses of protoplasm occupy the interstices between the tissues of the alga and contain many spicules, among which there are often fibuliform bodies like those figured by Schmidt for *Reniera fibulata* (Die Spongien d. Adriat. Meeres, p. 73, t. 7, f. 9). On the surface of the alga are found spicules which form a reticulum, and completely cover it with a pellucid pellicle. Schulze, who determined the sponge, was struck by the remarkable resemblance of the alga to *Chalina* and regarded it as a case of mimicry. Dr. Askenasy has recently published some interesting observations on *Marchesettia* with an illustration (Forschungsreise der 'Gazelle,' Theil IV. Botanik; Algen, Tab. xii).

We have very little doubt that these cases (Dr. Marchesetti's and our own) are of much the same nature as those recorded by Dr. Carter (Ann. and Mag. Nat. Hist. 1878, p. 163) whatever their true explanation may be. Dr. Carter's opinion, which is of the highest value, is that in the cases he records the seaweed gradually replaces and becomes what a mineralogist would term a pseudomorph of the sponge. He observed, for example, *Thamnoclonium flabelliforme*, which had replaced *Reniera fibulata*, and an unnamed alga, which had similarly treated *Halichondria plumosa*.

It should have been said that *Marchesettia* was collected at Singapore, and that it occurs also at Nosibè, Madagascar (Hildebrandt), and in New-Caledonia, the locality of *Spongocladia neocaledonica*, Grun. It is obvious that living material illustrating one or other of these cases need not be hard to find, and it may be hoped that the observations which alone can settle the matter will be made before long.

Professor Bayley Balfour has kindly called our attention to the case of *Spongia cartilaginea*, Esp., especially mentioned by Semper in his 'Animal Life,' (Internat. Sci. Ser.), p. 343. It is obviously of the same nature as *Marchesettia*, though the alga is a different one. Esper, in describing this remarkable association of sponge and alga (Pflanzenthiere; Fortsetzung, II. p. 23, Tab. LXIII), says that the alga agrees with '*Fucus corneus* or *cartilagineus*' = *Gelidium*

corneum, Lam., or *G. cartilagineum*, Gaill. Semper thinks that the sponge in this case 'may with some probability be included in the family of the Chalinae.'

GEORGE MURRAY, London.
L. A. BOODLE, London.

PRELIMINARY NOTE ON THE MORPHOLOGY AND DEVELOPMENT OF ISOËTES LACUSTRIS, LINN.—The genus Isoëtes has always been an object of interest to botanists ever since Hofmeister's brilliant researches on the vascular cryptogams, but the accounts given by the different observers on the development and organogeny of the sporophyte are so conflicting, and moreover our knowledge of the sexual generation is so limited, that a renewed investigation of the whole subject seems desirable. In the present communication I propose to summarise, as briefly as possible, the more important of my own observations on one species, *I. lacustris*, to which my attention has been directed for some time past. I intend to deal here only with the germination of the macrospore, and to reserve details of minor significance, as well as all account of the sporophyte, for treatment in a future paper, as this part of the subject requires critical discussion.

The shape of each macrospore is, as is well known, that of a tetrahedron with somewhat rounded sides, and the protoplasmic contents are enclosed in a number of coats which in mature specimens are differentiated into six layers. Peripherally is the episporium, a colourless, glassy, and brittle layer, whose surface is beset with numerous irregular prominences. The episporium which is derived from the epiplasm of the sporangium stains with haematoxylin, though only to a slight extent. Within this outer layer is the exosporium, consisting of three brown cuticularised layers, but of which the two outer ones are frequently not easily distinguishable as separate coats. The two innermost membranes are cellulosic in character and form the endosporium.

The protoplasm which is contained in the spore includes a large quantity of reserve-material consisting of starch and oil, the latter being, however, eliminated during the process of soaking in turpentine to which the spores are subjected previously to their being embedded in paraffin. A number of sections through each spore were obtained by means of the Cambridge rocking microtome, and were arranged in series, thus permitting of an examination of the internal structure of

the spores. The protoplasm, which is remarkably granular, is of a spongy texture (probably due to the extraction of the oil), and contains a nucleus of very large size in which bodies resembling nucleoli were in some cases detected. The nucleus is sharply marked off from the cytoplasm by a membrane, but it must be borne in mind that this feature may be due in part to the methods used in embedding. When spores are examined in this stage the protoplasm stains but slightly with haematoxylin, and the tint is inclined to red, even the nucleus not being deeply coloured. In somewhat older spores, at the period immediately preceding germination, the whole protoplasm stains far more readily and deeply, but a nucleus is no longer differentiated by staining, and the colour now produced is of a deep blue. As I have frequently had spores of different ages on the same slide, all of which were subjected to exactly similar treatment, this difference probably indicates an actual diffusion of the substance of the nucleus through the cytoplasm, since the change is always so prominent in spores in the condition referred to.

This view receives some confirmation from the circumstances attending the formation of the prothallium, now to be described. The first indication of cell-division occurs in a somewhat peculiar manner, but its significance is rendered clear by what takes place subsequently. Before entering upon a description of what actually happens, it may be well, in order to avoid misconstruction, to state expressly the opinion that the characters presented are rendered visible only by the action of the means necessarily employed in embedding. This does not, however, vitiate the conclusion that they may be taken as indications of internal changes which actually occur in the protoplasm. In spores, in which cell-formation is about to commence, the deeply stained protoplasm is seen to be traversed by a few 'cracks' which divide the contents of the spore into a few large isolated masses. Although the surfaces of the protoplasmic masses which abut on the 'cracks' possess a granular structure, there is nothing as yet which points to the definite existence of a cell-wall separating them from each other; at a subsequent period, however, the spaces ('cracks') are seen to be traversed here and there by membranes of extreme tenuity, which are also in contact with the protoplasm in numerous places. These membranes are formed in the spore between originally confluent masses of protoplasm, and the splitting is produced artificially as above referred to. The young cell-wall, very soon after its appearance, grows

in thickness, and is very easily recognised; but from the mode of its formation it can hardly arise otherwise than by the conversion of a layer, already present in the protoplasm, directly into cellulose, and it appears to be the presence of this substance, arranged in a definite plate-like manner, which determines the splitting referred to. The first membrane cuts the spore into an apical and a basal portion, and while the latter for some time undergoes no further change, the apical cell is divided almost simultaneously into a number of cells whose arrangement can still be followed even in quite old prothallia. When the first primary cells are formed, the nuclei are again distinguishable by haematoxylin, but they are of exceedingly small dimensions; and with this change the staining properties of the protoplasm become less marked. Divisions in all planes proceed very rapidly in the upper portion of the prothallium, and the rudiments of the archegonia are laid down much as in the *Marattiaceae*. Periclinal division of single superficial cells into two takes place, the upper of which gives rise to the neck, and by repeated division forms four stories, each story being divided into four cells arranged like quadrants of a cylinder. The lower cell gives rise to the central series, in which a neck canal-cell is cut off, and then a ventral canal-cell, from the oosphere. It can now be seen that the canal-cells thrust themselves between the neck-cells, and produce a distortion in the two lower stories so great that in some cases these are not easily recognisable in later stages.

While these changes have been taking place in the upper of the two primary cells, the basal one is dividing, but comparatively slowly, and it is easily distinguishable in that the cells which arise from it remain of a large size as compared with those formed in the upper part of the prothallium.

In spite of repeated search through a great number of preparations, it has not been found hitherto possible to arrive at a definite conclusion as to the mode of cell-division which prevails in the secondary stage, for no karyokinetic figures could be detected; nevertheless it is highly probable that the process does not differ in any important respect from that prevailing in other plants, and the arrangement of the nuclei about the walls of recently formed cells makes this supposition almost a certainty.

I have purposely omitted any reference to the researches of other observers in the present note, and it was not my object to attempt

a complete account of my own work, which is still in progress, but the results given above appear of sufficient interest to justify the appearance of this note.

J. BRETLAND FARMER, Oxford.

ON A NEW FORM OF TRAPELLA SINENSIS.—Since the account of the new Chinese genus *Trapella* appeared (ANNALS OF BOTANY, Vol. II (1888), p. 75) further specimens have been forwarded by Dr. Henry from Ichang. The specimens in question, which are dried, show an apparently unbranched, erect-growing, dwarf plant, which there is no reason to suppose is other than a terrestrial form of *T. sinensis*. The plant grows in amongst the rice-stalks in the locality where the aquatic form was taken. Its general configuration would point to the plant being a reduced form of the aquatic species, adapted to land habit. The leaves are smaller and of one shape, and the fruits are borne in the leaf-axils. The plant does not exceed 10 cm. in height. Dr. Henry was never able to find it in flower, and an examination of this material points to a cleistogamic production of all the fruits. It will be remembered that, in the aquatic form, all the fruits developing in the axils of *submerged* leaves are so produced. It is possible some difficulty attends the pollination by insects of normally expanded flowers, growing, as the plant does, crowded in between the bases of the rice-stalks. As to histological differentiation, such examination, as was possible, of the dried specimens, shows a retention of the aquatic type of central bundle-cylinder, with however a more powerfully developed xylem—there being several rings of vessels—than in the described form. For the present this form may be regarded as being derived from the normal aquatic type, recalling a comparable state of things in the genus *Myriophyllum*. Should Dr. Henry be able to send spirit-material of this plant it should furnish the basis of a supplementary paper on this singular genus. During the past summer, however (1888), no specimens of *Trapella* were observed, either in the rice-fields or in the ponds. The season was a very dry one, and the pond in which *Trapella* previously occurred was dried up.

F. W. OLIVER, Kew.

Pachytheca.

BY

SIR J. D. HOOKER, K.C.S.I., F.R.S.

With Plate VIII.

IN the year 1853 the late Mr. H. E. Strickland, F.R.S., communicated to the Journal of the Geological Society of London a paper entitled 'On the distribution and organic contents of the Ludlow Bonebed, in the districts of Woolhope and May Hill, with a note on the seed-like bodies found in it by Dr. J. D. Hooker.' The seed-like bodies in question, to which I subsequently gave the name of *Pachytheca*, were thick-walled, hollow spheres. They were smooth on the surface; their cavity was empty; and they were of an exceedingly brittle, carbonised substance, and so opaque that even with the aid of that skilful lapidary, the late Mr. Cuttell, I was unable to obtain any section that transmitted light.

The walls of the fossil appeared to consist of elongated cells radially disposed, and I concluded that *Pachytheca* might be the sporangium of a lycopodiaceous or allied plant, a conclusion assented to by the botanical and palaeobotanical friends who were so good as to examine the specimens with me, or for me.

Nothing further appears to have been known of the nature of *Pachytheca* until 1875, when specimens of it were communicated by the late Mr. R. R. Grindrod, of Malvern, to the Rev. Mr. Symonds, of Pendock, with the request that they might be submitted to me for examination. In a letter to myself Mr. Grindrod stated that he had himself knocked these out of

the West Malvern Wenlock Limestone; that he felt certain that the fossil was a lycopod, and proposed to have a section of one specimen made, but resolved not to do so until I had seen it. With Mr. Grindrod's permission I had sections of this specimen made, and these at once revealed to me the fact of the algal nature of *Pachytheca*; but, as to which, if to any, existing order of Algae it should be referred, I was and am unable to form any very definite opinion.

After examining the sections myself, I submitted them to various botanists and naturalists who had made a study of the lower order of plants, and especially to cryptogamists, who all assented to my conclusion as to the algal nature of the organism, but whose opinions as to its nearer affinities were very much at variance with one another.

There are three points in the general character of this fossil that are especially puzzling.

First, the perfectly spherical form of so many of the specimens, whether carbonised or calcified, that I have seen: and they are from various localities. This indicates either a density of tissues that has withstood compression, or the infiltration of a soft tissue by mineral matter during or previous to fossilisation. It further indicates a resistance to decay, for otherwise the minute tissues of the periphery would have been destroyed. Not only has the spherical form been perfectly preserved in all but obviously compressed specimens, but the peripheral ends of the radiating filaments, of which the wall of the organism is composed, have their lateral walls as perfect as are those of the inner cells; and this, though the apices of the peripheral cells are broken away all over the surface of the organism: which conditions seem to indicate that the whole surface of the latter has been abraded. There can, I think, be no doubt but that the substance of *Pachytheca* was dense and resisting to a remarkable degree.

The second character is the contrast between the tissues of the wall or cortical substance, and those of the filaments that traverse the central cavity in all directions. From the first I have been disposed to regard these latter filaments as having

no organic connection with the cortical, and as indeed belonging to an intruded parasitic alga, or the mycelium of a parasite—an opinion shared by several algologists. I could find no connection between these and the cortical portion, nor could Mr. Busk nor Dr. Lankester, who have both examined the specimens.

The third point is the total absence of any point of attachment on the surface of the specimens, or of any indication even of such. Nor is there any indication in the arrangement of the tissues, of growth from a definite point. I have only further to remark under this head that no specimens showed any trace of organs of fructification.

In 1882 Principal (now Sir William) Dawson communicated to the Geological Society of London 'Notes on *Prototaxites* and *Pachytheca* discovered by Dr. Hicks in the Denbighshire Grits of Corwen, N. Wales.' I was then absent in Italy, but Mr. Dyer, having access to my sections of *Pachytheca*, communicated the latter to Mr. Judd, the President of the Society, for exhibition at the meeting, with a note to which I shall hereafter refer.

At that meeting Sir J. W. Dawson expressed the opinion that *Pachytheca* was more probably a seed than a spore case, and that it has the structure of *Aetheotesta*, to which genus he had previously referred a similar seed found in the Devonian of Scotland. In another paper, he mentions similar bodies to *Pachytheca* being found in a pyritised state in the Upper Silurian of New Brunswick, associated with the wood of *Prototaxites*; and adds that these specimens 'though on the whole less perfectly preserved as to structure than the Welsh specimens, when sliced in certain directions they present traces of a micropyle and embryo, and are probably true seeds.'

In still another paper Sir J. W. Dawson repeats his opinion as to there being little doubt that the New-Brunswick and Corwen specimens may be referred to Brongniart's *Aetheotesta*: and he points out, as worthy of note, that Brongniart says of his *Aetheotesta subglobosa* from the Coal-measures, that the

testa is thick, homogeneous, formed of fibres or elongated cells perpendicular to the surface; and that these fibres appeared in the specimen to be intermixed with globular cells, possibly in consequence of alteration of the tissues. Sir J. W. Dawson goes on to say that this is precisely the appearance presented by the testa *Pachytheca*; that Brongniart's *Aetheotesta* is undoubtedly a seed, and that the latter author compares it with the nut-like seeds of *Taxineae*. Sir J. W. Dawson concludes by saying that, as *Pachytheca* has been found in both England and North America associated with *Prototaxites*, and since the structure of the Corwen specimen of *Pachytheca* corresponds with that of *Prototaxites*, the presumption becomes strong that the connection is not accidental, and considering the Taxine affinities of *Aetheotesta*, *Pachytheca* affords some corroboration of the gymnosperm nature of *Prototaxites*.

In the discussion that followed the reading of Sir J. W. Dawson's paper Mr. Carruthers stated that he thought I was justified in referring the carbonised specimens of *Pachytheca*, which I had first seen, to *Lycopodiaceae*; but having himself examined beautifully-prepared sections of *Pachytheca*, and found the cellular structure filling its interior, he was inclined to doubt its being really a vegetable, and wished that zoologists would examine it.

Mr. Carruthers was followed by Dr. Martin Duncan, who did not regard the central part of *Pachytheca* as a mycelium, but regarded the whole organism as the float or conceptacle of a seaweed.

Mr. Dyer's letter accompanying my specimen was then read, in which he said that he had come to the conclusion that the structure of *Pachytheca* agreed in general plan with that of *Codium*, but with the peripheral walls branched instead of simple: and that *Prototaxites* and *Pachytheca* are referable to the same morphological type of structure; but that there is no evidence of the latter being a sporangial organ of the former. He further stated that the radiating cells of *Pachytheca* terminated in the loosely-interlacing, slender filaments of the central cavity. This organic connection between the tissue of

the cavity and walls is, if confirmed, a fact of great importance. It has escaped my own notice and that of several excellent observers, who had devoted much time to the study of my specimens.

A very able algologist, who has most carefully examined the specimens, Mr. Phillips, of Shrewsbury, regards *Pachytheca* as a *Rivularia* with the cavity invaded by an *Oedogonium*. I had from the very first considered the possibility of such an explanation, but was and am deterred from accepting it from the difficulty of supposing that a flaccid freshwater alga of the nature of *Rivularia* could have retained its spherical form under fossilisation; and by the fact of the form of the enlarged cells terminating the peripheral filaments towards the centre.

Another genus that shows some similarity to *Pachytheca* in the disposition of its filaments is *Mazaea rivularioides*, which forms globular or sub-globular hollow bodies of radiately disposed branching filaments in which the cells enlarge towards the periphery. The cavity in this genus is, however, the result of the decay of the inner terminations of the filaments. The filaments of *Mazaea* further bear heterocysts on their sides, of which there are no traces in *Pachytheca*.

Professor Balfour has suggested that the form of *Pachytheca* is somewhat like a *Chaetophora* with an incrustation of lime. Finally Solms-Laubach, on page 124 of his 'Einleitung in die Palaeophytologie' recently published, writing of Pachytheca says, 'I entertain some doubts as to the vegetable nature of these remains.'

Such are the principal views hitherto held as to the nature of *Pachytheca*. From this it appears that until some much closer counterpart of the tissues of that organism than has hitherto been found among existing plants have been discovered, it is in vain to speculate on its near affinities; and that until the peripheral termination of the filaments composing its walls and its organs of fructification are made known, no certain conclusions as to its real nature and affinities are possible.

EXPLANATION OF FIGURES IN PLATE VIII.

Illustrating Sir J. D. Hooker's paper on *Pachytheca*.

[The figures on this plate are reproductions of very careful drawings of sections of a *Pachytheca* made by myself under the microscope many years ago. The specimen itself has unfortunately been lost; it differs from that which forms the subject of Mr. Barber's paper in its much thicker walls, smaller cavity, and in the more numerous large cells in several series towards the interior, as also in the more evident passage of them into the cells of the radial tissue. The drawings were compared with the specimen by many observers, and may be confidently regarded as accurate representations.—J. D. H.]

Fig. 1. Three specimens of *Pachytheca* of the natural size.

Fig. 2. Transverse section of the larger of them.

Fig. 3. Segment of *Pachytheca* from the centre to the circumference.

Fig. 4. Portion of four radiating fibres of the periphery.

Fig. 5. Portion of the periphery from another specimen, in which the filaments are separately imbedded in the mineral matrix.

Fig. 6. Greatly enlarged view of the cells towards the central cavity of the *Pachytheca*, and filaments from the central cavity, showing their relative dimensions.

Fig. 7. Similar cells still more enlarged.

Fig. 8. Filaments from the central cavity.

Figs. 9–12. Transverse sections of filaments in the central cavity.

Figs. 2–12 all more or less enlarged.

Fig. 1.

Fig. 2.

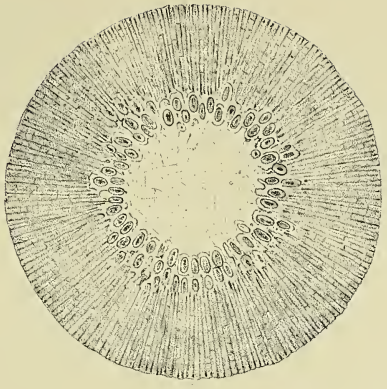


Fig. 3.

Fig. 4.

Fig. 5.

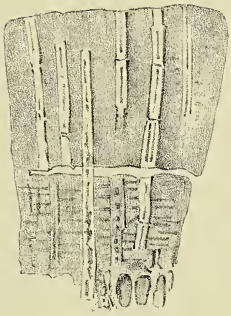


Fig. 7.

Fig. 6.

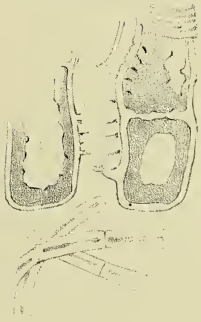


Fig. 9.

Fig. 10.

Fig. 11.

Fig. 12.

Fig. 8.

J. D. Hooker del.

University Press, Oxford.

HOOKER.—ON PACHYTHECA.

The Structure of Pachytheca.

BY

C. A. BARBER, B.A.,

Scholar of Christ's College, Cambridge.

With Plate IX.

TOWARDS the end of 1887 two slides containing sections of *Pachytheca*[1] were placed in my hands by Sir Joseph Hooker, and I have prepared the following account of the structure of the plant, with the accompanying figures as an adjunct to his preceding account.

Of the two sections only one appears to pass accurately through the centre of the organism; the other appears to pass through the middle of the spherical body at a short distance from the centre. For clearness' sake, the description will be mainly based upon the first of these two slides.

There are three zones to be distinguished in the specimen: an outer *cortical zone* composed of parallel radiating filaments separated by a clear, slightly-coloured mineral matrix; a *central part*, consisting of a colourless mineral matrix penetrated by filaments in different directions; and a *zone of oval bodies* separating the cortex from the central part (Figs. 1, 2).

In the *cortex* (Figs. 2, 3, 4) the radiating filaments are divided into cell-rows by transverse walls. The appearance of a filament, generally, is similar to that of a *Cladophora*. The ends of the peripheral cells are not present, since these are broken off at various points, and the specimen appears to have been abraded. Branching is not at all common. In two or

[1] These are not sections of the specimen, the figures of which (Plate VIII.) accompany Sir J. Hooker's paper.

[Annals of Botany, Vol. III. No. X. May 1889.]

three cases, however, there is undoubted branching (Fig. 4). The cell-rows are separated from one another by a slightly-coloured matrix, and the distance between two adjacent cell-rows is as great, or slightly greater than the diameter of one of the cells. On the transverse walls are developed oval swellings, similar to the callus-plates or 'stoppers' of the Florideae or the swellings on the walls of *Oscillatoria* or *Nostoc* (Figs. 3, 4).

In the *central part* the filaments are also divided by transverse walls: they appear to penetrate in all directions a clear colourless matrix (Figs. 2, 5, 6, 7). In the section some appear to be cut transversely, and others obliquely, while some appear to run in the plane of the section. There is no well-marked branching; and the stoppers appear to be absent from the transverse walls. The cells appear to be slightly less in diameter than those of the radiating filaments.

It is at present impossible to say whether the cortical and central filaments are continuous. The filaments from the centre appear to have no connection with the oval bodies, but appear distinctly to wind in between them (Figs. 6, 7); and on tracing the filaments from the cortex inwards they also appear to pass between the oval bodies (Fig. 6). From the figures it will be seen that a direct continuity between the filaments of the different zones cannot be assumed. The walls of a cortical filament sometimes appear to be continuous with those of two contiguous oval bodies, while the central filaments appear to push themselves in between these latter. If this be so, the central filaments push themselves inside the cortical. There is, on the other hand, one case where an oval body appears distinctly to branch outwards into two radiating filaments, but it is not safe to lay stress on any isolated example.

The main difficulty lies in the *zone of oval bodies*. Their shorter diameter is three or four times as great as that of the cortical filaments, while their length varies considerably (Figs. 2, 6, 7). In all cases there are well-marked inner walls separating them off sharply from the central matrix; but towards the cortex there is no such sharply-marked

boundary. Their colour approaches that of the spaces between the cortical filaments, while that of the spaces between the oval bodies themselves is frequently similar to that of the central matrix.

At first sight the oval bodies appear to be swollen cells which give rise by branching to fascicles of radiating filaments, and there is at least one case which seems to support this view. In the majority of cases, however, they would appear to be the spaces between filaments, and they appear to be continued outwards into the slightly-coloured matrix separating the cortical filaments. There are at present great difficulties in the way of this latter view. The distinct wall separating them from the central matrix is never double; and it would undoubtedly be double if the oval bodies were merely spaces separating filaments. Again, in the section, the oval bodies appear to be separated by wide spaces from one another; and these spaces are bridged across by parallel bars distinctly continuous with the walls of the oval bodies (Fig. 6). The central filaments appear to wind in and out between these bars. It would be difficult to imagine that the cortical filaments suddenly lose their filamentous character and expand into these spaces. Finally, in the second section, which seems to pass at some distance from the centre, we meet with some of the oval bodies cut across (Fig. 7). They appear to be circular in section, and have a well-marked wall surrounding them. They are separated from each other by irregular spaces, and the latter show no signs of being formed by cells—as would be the case if the circular bodies represented merely the spaces between cell-filaments.

From what has been said, it will be at once clear that nothing decisive has been learnt regarding the systematic position of the organism. That it is an alga seems to be now generally conceded; and it probably grew on the sea-bottom, where it rolled to and fro in the passing eddies.

The presence of transverse walls indicates that it is not one of the *Siphoneae*; the branching appears distinctly of a higher order than that of the *Cyanophyceae*; and the presence

of the 'stoppers' appears to indicate a comparatively highly differentiated organism. One of the questions of greatest interest is, whether we have here to deal with a single plant or a case of symbiosis or parasitism. If all the cell-filaments and the oval bodies belong to one organism, the plant is, I believe, without parallel among existing Algae. If, on the other hand, the central filaments prove to be parasitic on, or symbiotic with, the rest of the parts, we are not altogether without similar cases. Mr. Thistelton Dyer has referred me to a species of *Rivularia* which is penetrated in a similar way by a *Cladophora*. This species, which occurs in Belvedere Lake, Mullingar, further resembles *Pachytheca* in its possessing a stony consistence: it forms small round pebbles on the bottom of the lake.

It is, however, easy to construct any number of hypotheses regarding so puzzling an organism. The oval bodies may be regarded as being the skeleton of a siphonioid form, and the possible resemblance to *Cymopolia* has been suggested. Until further sections are obtained it does not appear probable that there will be any easy solution of the matter.

In conclusion, a curious resemblance may be pointed out between the section of *Pachytheca* and a transverse section of the stalk of *Furcellaria fastigiata*. In the latter section there are three zones as in *Pachytheca*: a central portion containing a colourless matrix penetrated in all directions by cell-filaments; a cortical zone of radiating cell-rows; and a zone of large spherical cells separating the two. The cortical cells are continuous with the zone of spherical cells, but the cells of the central portion appear at first not to join the latter. On the contrary, they evidently push themselves in between the spherical cells. There are, as in *Pachytheca*, numerous bars stretching between two neighbouring spherical cells, and the penetrating central filaments appear to wind in between these bars. There appears at first to be no connection between the central filaments and the spherical bodies; a longitudinal section at once shows, however, that each spherical body is connected with a cell of the central portion

which passes obliquely into it, so that the connection is hidden in a transverse section.

The sections upon which the foregoing account is based being manifestly insufficient for a definite statement as to the systematic position of the plant, it occurred to me, while on a visit to Norton in Shropshire, in June 1888, that I might obtain some more specimens of *Pachytheca* from the rocks of the neighbourhood, which form the transition between the Silurian and Old Red Sandstone; and accordingly I set to work to examine the Downton Sandstone, so extensively quarried in this district as building stone. In the study of these rocks I was greatly assisted by the Rev. J. D. la Touche, of Craven Arms, who also placed in my hands a specimen of rock containing *Pachytheca*.

The result of my examination was that, in every one of the half dozen quarries explored, *Pachytheca* was found either in a carbonised or pyritised state; and it was usually accompanied by *Lingula cornea*, fragments of Crustaceans, small pieces of carbonised 'wood,' and other organic remains. The quarries examined were those at Norton, Onibury, and Forge Bridge near Downton Castle. In most of these the rock is no longer worked, and I was dependent for my specimens on loose pieces of stone; but in the fine new quarry in the Aldon Lane, near Onibury, I succeeded in finding many specimens of *Pachytheca* in situ. And I am satisfied that the plant is not confined to one horizon, but occurs at numerous different levels, being especially abundant in the thin layers between the massive courses of fine stone.

My attention was next directed to the Woolhope district, in which Strickland long ago detected *Pachytheca*. I was only able to spend one day in this neighbourhood, but, in the Perton Quarry, near Stoke Edith, I found *Pachytheca* in great abundance. Specimens from all these localities, together with a remarkably resistant one from the passage beds at Ledbury, were submitted to the best London lapidaries for cutting. In all specimens which allowed of grinding, the cortex turned out to be pyritised, and I was consequently

unable to detect any structure in the sections by transmitted light.

I was unable to visit the Wenlock Limestone near Malvern, in which Mr. Grindrod found his specimens[1]; nor was I able to visit Corwen quarries, where Hicks found silicified specimens of *Pachytheca* and *Nematophycus* showing structure. Mr. Carruthers, of the British Museum, tells me that *Pachytheca* has also been obtained from the passage beds at Cardiff, and that sections have been prepared of specimens, which exhibit structure.

In the best specimens I obtained it is perfectly easy with the naked eye to detect the radiating character of the elements composing the wall or cortex of the organism (Figs. 9 and 10). In such specimens the cortex is black in colour, while the central part is filled with white crystalline powder.

As was pointed out to me by Mr. La Touche, there is in most specimens a depression on one side of the rounded body (Figs. 8 and 8 *a*). Mr. Phillips, of Shrewsbury, has suggested that this depression might indicate the point at which the plant was attached to foreign bodies, much as *Rivularia* is now found adhering to sticks. The depression might be due to the collapsing of the wall of the hollow organism; this could only occur before the walls assumed the resistant nature which has rendered preservation possible. There does not appear to be any discontinuity of the filaments at this point.

In several cases I found small *Pachytheca*-like bodies arranged in rows of four or five (Fig. 14). The occurrence of such a condition was not, however, common enough for any general conclusion to be drawn from it.

The centres of the pyritised specimens are usually of a crystalline nature. The diameter of this portion, however, as compared with that of the whole organism, varies very considerably. In some specimens the cortical portion is of such extent that no space is left in the centre for the crystalline matter. In others again the dark cortex appears as a thin

[1] Three days careful examination of the West Malvern Wenlock Limestone in January 1889 produced no further specimens of *Pachytheca*.

peripheral band, and the crystalline centre has a diameter fully three-fourths of that of the whole sphere. There is not usually any structure to be made out in the central part; but in one case it appears to have distributed through its substance numerous dark dots. Finally, in one specimen, whose section appears on the surface of the stone, there appears to be a second dark ring at some distance from the cortex, and completely surrounding it.

It may be noted that the only specimens showing the microscopical structure described in this paper were found in the Wenlock Limestone: and the only reasons we have for regarding these bodies as identical with such as are frequently met with in the Transition Beds, are their spherical shape, and the general arrangement of the filaments composing the cortex. The *Pachytheca* of the Bone-bed and the Downton Sandstone appears to differ from that of the Wenlock Limestone in certain particulars; and a comparison of the drawings made from specimens obtained in the sandstones, illuminated by reflected light, with the transparent sections from the Wenlock Limestone, suggests that we may have to do with two entirely different organisms[1]. In no specimens from the Downton Sandstone have I found any trace of the circular spaces at the base of the radiating filaments, which form so puzzling a feature in the sections from the Wenlock Limestone possessed by Sir Joseph Hooker. As far as can be judged from the sandstone specimens, the radiating dark lines do not swell out much at their inner ends, nor do they embrace circular spaces (Figs. 11, 11 *a*, 11 *b*).

[1] Since writing this paper I have had the opportunity of examining a section of *Pachytheca* from Corwen, which is preserved in the Jermyn Street Museum. Although the structure is not very well shown, a comparison certainly strengthens the suggestion that several different organisms have been included under the name of *Pachytheca*.

DESCRIPTION OF FIGURES IN PLATE IX.

Illustrating Mr. C. A. Barber's paper on the structure of *Pachytheca*.

Figs. 1–7 are drawn from sections in the possession of Sir Joseph Hooker, made from specimens obtained in the Wenlock Limestone. By transmitted light.

Figs. 8–14 are drawn by reflected light from carbonised or pyritised specimens obtained in transition sandstones.

Fig. 1. Slide 1. Section of *Pachytheca* magnified; Fig. 1 *a* natural size.

Fig. 2. Portion more highly magnified.

Fig. 3. Portion of cortex highly magnified.

Fig. 4. Portion of cortex showing branching filament.

Fig. 5. Portion of centre.

Fig. 6. Portion of zone of oval bodies: Figs. 3, 5, 6 about the same enlargement.

Fig. 7. Slide 2. Portion of zone of oval bodies.

Figs. 8, 8 *a*. *Pachytheca* natural size from Forge Bridge and Onibury.

Fig. 9. *Pachytheca* broken in half, magnified.

Fig. 10. *Pachytheca* and 'wood,' probably *Nematophycus*, natural size.

Fig. 11. The same specimen magnified.

Fig. 11 *A*. Outer, and Fig. 11 *B*, Inner endings of filaments more highly magnified.

Fig. 12. Free surface of *Pachytheca*, magnified, showing endings of radiating fibres.

Fig. 13. Section of *Pachytheca* ground on a wrought-iron plate.

Fig. 14. *Pachytheca*-like bodies occurring in rows. × 2.

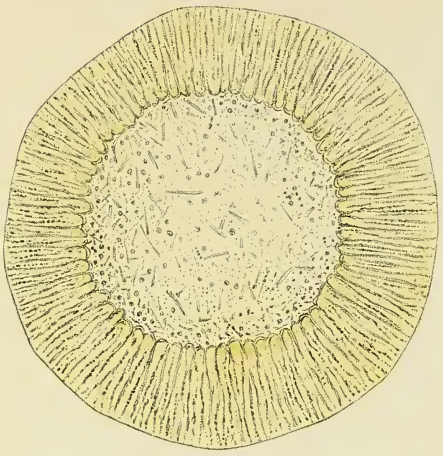


Fig. 1.

a

Fig. 12.

Fig. 13.

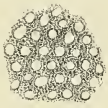


Fig. 14.

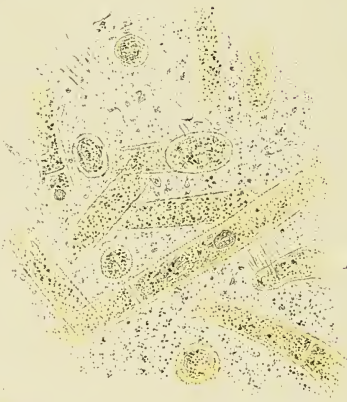


Fig. 5.

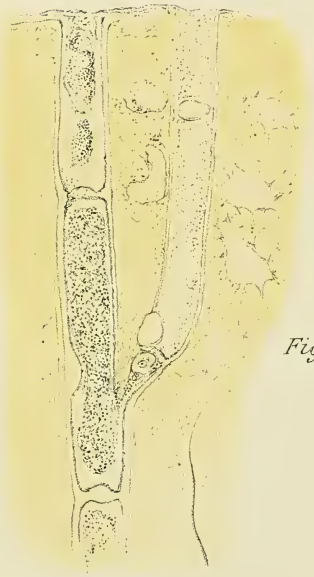


Fig. 4.

Fig. 7.

Fig. 2.

Fig. 3.

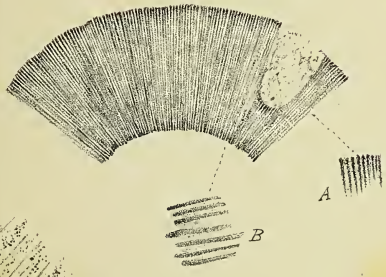
Fig. 10.

Fig. 9.

a

Fig. 8.

Fig. 11.



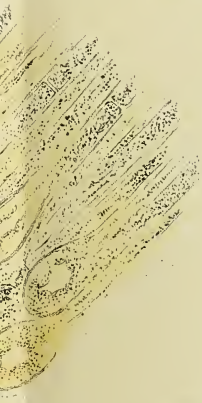


Fig. 6.

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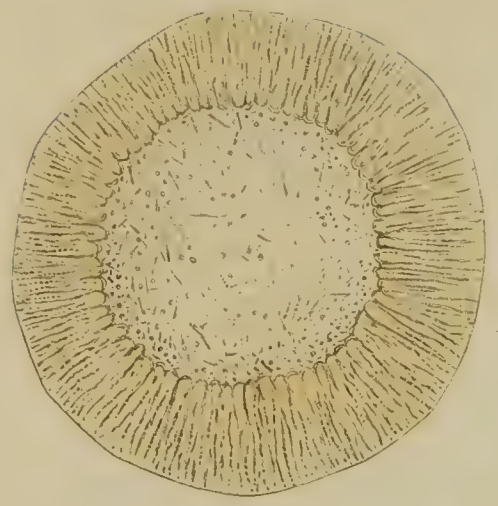

Fig. 1.

a

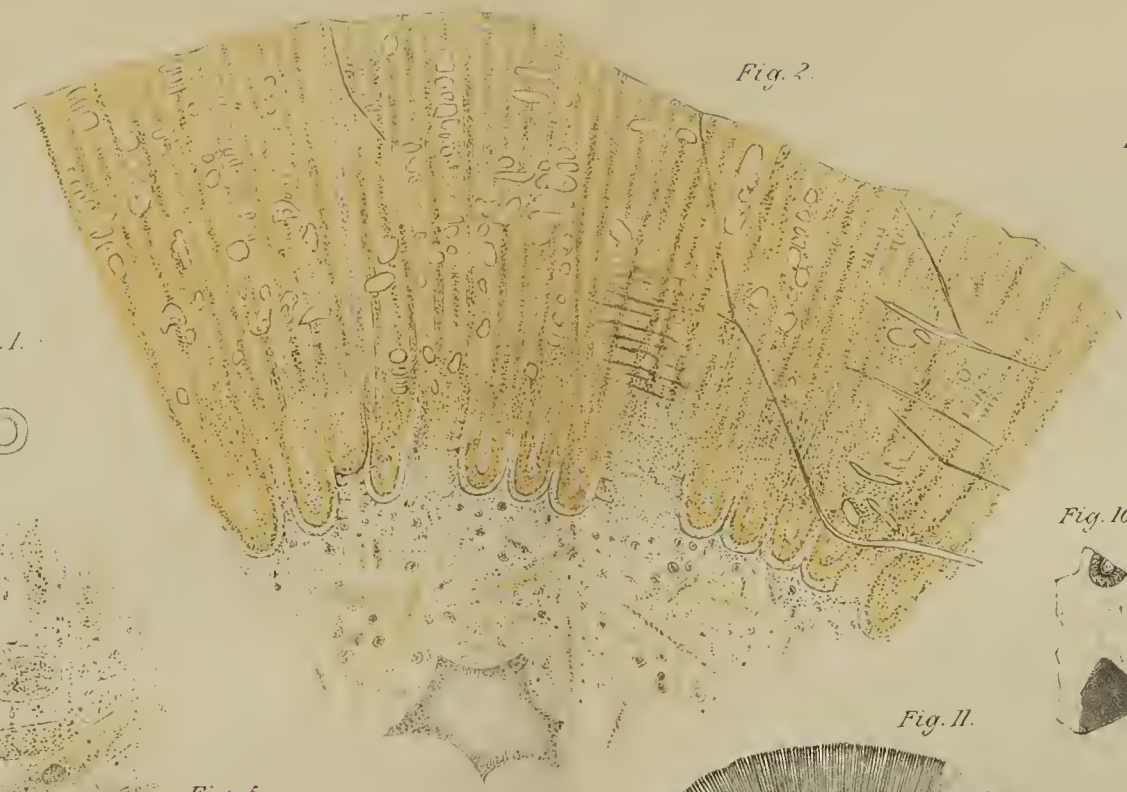

Fig. 2.

Fig. 3.

Fig. 10.

Fig. 12.

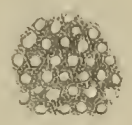

Fig. 13.

Fig. 14.

Fig. 5.

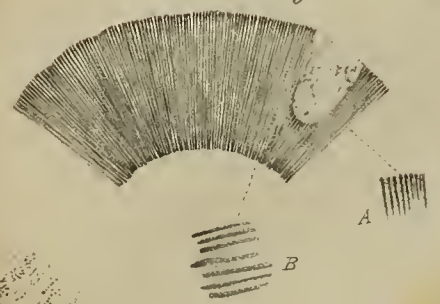

Fig. 11.

A

B

Fig. 9.

a

Fig. 8.

Fig. 4.

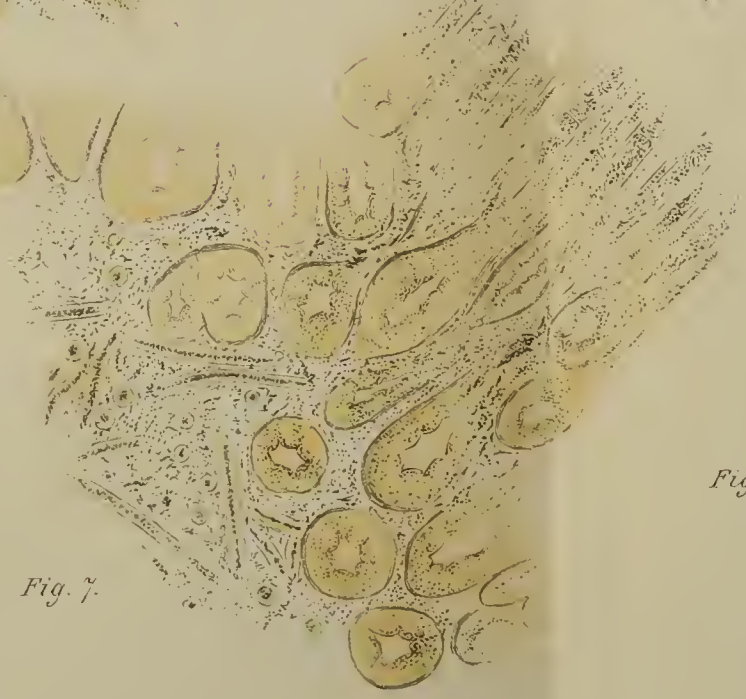

Fig. 7.

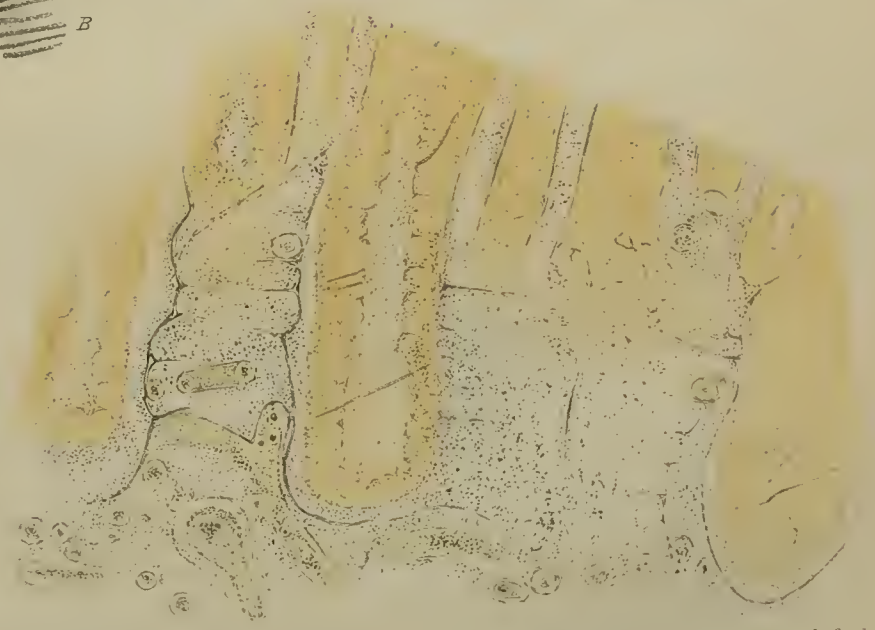

Fig. 6.

C A Barber del

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BARBER. — ON PACHYTHECA.

The Source of Badsha, or Royal Salep.

BY

J. E. T. AITCHISON, M.D., C.I.E., F.R.S.

With Plate X.

WHEN accompanying the Afghan Delimitation Commission during 1884, I carried with me some specimens of what is known as Badsha Salep, hoping to be able to discover the plant yielding it, and thus extend our limited knowledge of this little-known drug. In the vicinity of Herat, and at Meshed, I showed the product to many who might be likely to give me information regarding it, but it appeared to be quite new to all to whom I applied for the information.

Upon examination at Kew of the various substances which I had obtained whilst on my Afghan journey, to enable me to read a short summary regarding the drugs I had collected in those regions before the Pharmaceutical Society of London, I chanced to show some specimens of this Salep to Mr. Baker, who drew my attention to Mr. Daniel Hanbury's article in the Pharmaceutical Journal and Transactions for April 1, 1858. From the evidence which this article afforded there could be no doubt that my specimens were identical with those so well depicted and described by Mr. Hanbury.

Mr. Baker, at the meeting of the Pharmaceutical Society on December 8, 1886, at which I read my paper, was of opinion that he had identified the bulb as that of *Ungernia trisphaera*, a plant of the order Amaryllidaceae. This, however, was an error due to the bulb that he examined having been

[Annals of Botany, Vol. III. No. X. May 1889.]

wrongly labelled; and also owing to its being an only live specimen (the undetermined species of *Allium* of mine from Afghanistan hereafter referred to) a close inspection was not permissible; but, I think, almost the very next day the error was detected, after another more careful inspection of the wrongly-labelled bulb, which subsequently Mr. Baker and I were both satisfied was that of an *Allium*, and one very likely to represent in a dried state the form of Salep now under consideration.

During 1881, Dr. Wilson Johnston, F.R.S.E., of the Bengal Medical service, placed in my hands at Kew, for identification, a collection of plants from Afghanistan that had been made on the line of march between the Kojak Pass, Kandahar, and Cabul. In this collection was an *Allium* to which was attached the note 'Plant said to yield Salep in these parts.' When identifying this collection I had not heard of Badsha-Salep, and the above note I had utterly forgotten when investigating the subject during 1886. Only some months subsequently did I remember it, in connection with a large-bulbed herbarium-specimen of my own, belonging to my last Afghan collections.

During October 1888 I was in Edinburgh, and upon visiting the Royal Botanic Garden there, I asked Professor Bayley Balfour, the Keeper of the Garden, if he could show me a living bulb of *Allium Macleanii*. Not only did he do so, but most liberally presented me with two specimens of it. The moment I handled the bulb of this species, I recognised at once that there could now be no doubt as to this being the living condition of the dried product under discussion.

The original specimens at the Edinburgh Garden came from Mr. Wilson of St. Andrews, who had received them from Colonel (now General) Maclean, C.B. from Afghanistan, with a note attached, stating that they were given to him by an Afghan chief as the plant that yielded Salep. Mr. Wilson also sent a flowering plant to the Royal Gardens at Kew, which afforded material for its description and delineation as a new species by Mr. Baker in the Botanical Magazine, Plate

6707; but in Mr. Baker's description there is no notice taken of its being a plant said to yield a kind of Salep.

Upon handling the living bulb of *Allium Macleanii*, Plate X (Fig. 4), at this stage of its growth, I found, with the exception of where there still remained adherent some slight shreds of a cast-off membranaceous scale (Fig. 4, *f*, *f*), that the surface had a glistening semi-transparent appearance, and that the bulb felt hard, dense, and solid. On one side of the external surface there is a groove more or less apparent, broadest at the greatest circumference of the bulb, narrowing towards the base, where it occupies about one-fifth of the circumference, gradually becoming lost towards the apex, by narrowing off to a sharp point; dividing this groove into two is a raised convexity passing from the base upwards, and most marked at the centre of the bulb. This convexity may be again divided by a slight groove.

A vertical section (Fig. 5) of the bulb, at this stage of its growth, shows a uniform mass (*c*, *c*) of tissue, having a potato-like consistency, in the centre of which a cavity exists (*d*, *d*), and at the base and in the centre of this cavity is the growing axis of the scape with leaves (*e*, *e*) springing from the flattened stem. On a transverse section (Fig. 9), the bulb is seen to consist of an external epidermal layer (*h*, *h*), continuous in tissue with the comparatively dense tissue (*c*, *c*) and a central hollow or cavity (*d*, *d*) containing the growing axis (*e*, *e*). The markings on the external surface of the bulb are not traceable into its interior structure, and except the shreds of a single membranous scale (Figs. 4, 5, *f*, *f*), no signs whatsoever are to be perceived of any other tunics.

By careful comparison of the bulbs of the following species of *Allium*, for permission to examine which I am indebted to the courtesy of Mr. Thiselton Dyer, C.M.G., the Director of the Royal Gardens, Kew, viz. of *A. giganteum*, Regel; *A. stipitatum*, Regel; *A. Suworowi*, Regel, and an Afghan undetermined species of my own, I have been able to ascertain that the characters above described in *A. Macleanii*, exist in these Central Asian and Afghan species. By examination of

them in a more mature stage, I find further that the growing axis (Fig. 7, *e*, *e*) ascends through the bulb, first of all filling up the central cavity, and then forcing its way upwards through separating the structures of the bulb. In some of the bulbs the apex (Fig. 6, *g*; Fig. 7, *g*) was seen to consist of two points, being cleft to a greater or less extent. The sap in some of the bulbs, when brought into contact with the oxygen of the air, became highly coloured, an orange yellow in *A. giganteum* (Fig. 7), and brick-red in the undetermined species from Afghanistan (Fig. 6), whilst that of the others remained unchanged. The sap of the roots, where the flattened stem was divided, and where the sap escaped from the cut surface of the leaves and scape took on the colouring, the cut surface of the solid part of the bulb was scarcely affected, but remained almost its original colour.

The development of this bulb structure will form an interesting physiological study for future investigation; but at present, owing to the limited amount of material at hand, the elaboration of the subject has to be postponed.

Professor Bentley, in his remarks upon Mr. Daniel Hanbury's paper, where indeed he foretold that in all probability this product would prove to be an *Allium*, noted that some of the commercial bulbs had a strong alliaceous odour, whereas in others no such odour could be distinctly traced. Now, it is a remarkable fact that in handling the fresh bulbs of *Allium Macleanii*, *A. giganteum*, and the Afghan undetermined species, there was no alliaceous odour to be detected. On sections of *A. Macleanii* being made there was still almost no trace of any alliaceous odour, though there was the odour, as one of the examiners remarked, 'of the remains of an old mustard plaster,' with a slight pungency; and this chiefly from the surfaces where the leaf-shoots and growing axis had been divided, rather than from the consolidated part of the bulb. Again, in the sections of *A. giganteum* the solid portion when freshly divided smelt somewhat like a newly-cut potato, and the alliaceous odour on the section of the leaves was much more obvious than in *A. Macleanii*; but this might be greatly

due to its more advanced stage of growth. But in both the alliaceous odour was certainly localised to the growing axis and young leaves. Whereas the bulbs of *A. stipitatum* and *A. Suworowi*, whilst still entire, gave forth a powerfully alliaceous odour, greatly intensified upon section.

In all probability the bulbs of more than one species of *Allium* are collected as Badsha-Salep. The size of these dried bulbs varies very greatly; this difference in size can, I think, be better accounted for by difference of species than by simple individual variation, when the product is, as in this instance, not that of a cultivated plant.

In the Museum at Kew there is a large specimen of a dried bulb called 'Giant Salep' from Bombay, presented by Mr. R. G. Clements, of which a smaller specimen is represented in Fig. 3. Another, presented by Major Hobson, from the East Indies, native name 'Amber-kund,' with the note 'Considered by the natives a valuable medicine in cases of consumption' (Fig. 1). Also a collection of smaller bulbs, of which a type specimen is given in Fig. 2, from the Indian Museum collection[1]. The last are highly alliaceous in odour, which at once apparently led to their identification, the others are all without odour.

Microscopic preparations are easily made from the Badsha-Salep by soaking in water. These exhibit a structure similar to that seen in species of *Allium*, and almost identical with sections made from the bulb of *Allium Macleanii*; the only difference being that the utricular vessels seen in the sections made from Badsha-Salep are densely packed with a yellowish granular substance of which there is little, though some, to be seen in the utricular vessels of the fresh bulb. Its smaller amount in the latter is to be accounted for thus: upon having made sections (not microscopic) of the fresh bulb they were at once placed in rectified spirits. No sooner was this done, than the spirit seemed to extract the contents of the fresh bulb, as a continuous stream of the most exquisite opalescent rose-colour.

[1] Labelled, No. 21. Materia Medica, No. 5 in Pharmacopoeia of India. Punjabee 'Piaz.' *Allium* Species, N.W.I. Prov. No. 3737.

This occurred some days before microscopic preparations were made of the tissues, and hence I believe the absence from the utricular vessels of the densely-loaded condition present in the vessels of the Badsha-Salep. That the sections of the fresh bulb had lost most of their contents might be seen by their shrivelled-up and contracted condition, after having lain a few days in the spirit. Dr. Macfarlane, who kindly prepared the microscopic sections at Edinburgh, thinks with me that in all probability the granular matter that so fills these utricular vessels yields the mucilage, on account of which the bulb is employed as a Salep.

In conclusion, the results of my investigations as to the source of Badsha or Royal Salep may be summed up in a few words. That we know a species of *Allium*, the bulb of which is considered by the natives of the country where it grows, to be a Salep; that the fresh bulbs of this, in general appearance and in microscopic structure, correspond to certain specimens of a drug known to us as Badsha-Salep. That all these specimens of the dried Badsha-Salep, though varying in size and odour, appear equally to be the products of an *Allium*, and that the differences which exist in the bulbs may be fully accounted for by difference in species.

As far as we know at present, the trade in Badsha-Salep seems to lie between Southern Afghanistan and India; in support of this I could hear nothing of the product, nor was it known near Herat or Meshed, the great centres of trade of North-West Afghanistan and North-East Persia; and that it is conveyed by Afghans along the various routes to India, chiefly to Bombay and Karrachi, as well as to Lahore and Simla, at both of which places I have myself obtained it.

The little knowledge we have of the distribution of *Allium Macleanii* is, that it was sent from Cabul, and Dr. Wilson Johnston's *Allium* 'said to produce Salep' was collected in Afghanistan on the route between the Kojak Pass, Kandahar, and Cabul. In all likelihood the latter was collected in the same locality as the former, as both officers were with the same expedition.

Since this paper was in print I have been able to come across a list of the plants that I identified at Kew for Dr. Wilson Johnston, and find that his Nos. 5, 17 were *Allium robustum*, Kar. et Kir., with the note 'Salep-misree'; besides his No. 3 (bulbs only), which were the bulbs of an Allium, collected on the Altimore pass in April 1880, and which he had noted as 'Orchis, Salep-misree.' Some of these bulbs were alive and were handed over to the gardens at Kew.

EXPLANATION OF FIGURES IN PLATE X.

Illustrating Dr. Aitchison's paper on Badsha, or Royal Salep.

Fig. 1 *a*, Shows the specimen of 'Amber-kund' in the Museum at the Royal Gardens, Kew, with a separate drawing of the base, *c*, and apex, *b*.

Fig. 2 *a*, Specimen of 'Piaz' from the Indian Museum, now at the Museum, Royal Gardens, Kew. *b*, A separate drawing to show basis of *a*.

Fig. 3. One of the smaller specimens of 'Giant Salep' from Bombay, at the Museum, Royal Gardens, Kew.

Fig. 4. A bulb of *Allium Macleanii*, Baker, in growing condition, received from the Royal Botanic Garden, Edinburgh, Oct. 12, 1888.

Fig. 5. Section of bulb of *Allium Macleanii*, Baker, made at the Royal Botanic Garden, Edinburgh, on Oct. 23, 1888, in the Museum of which the specimen now is.

Fig. 6. Bulb of an undetermined species of *Allium* collected in Afghanistan, 1885, which has been in the Royal Gardens, Kew, but has not as yet flowered. The rootlets on injury and exposure to the air changed their colour to brick-red. *f. f.* fragments of scales.

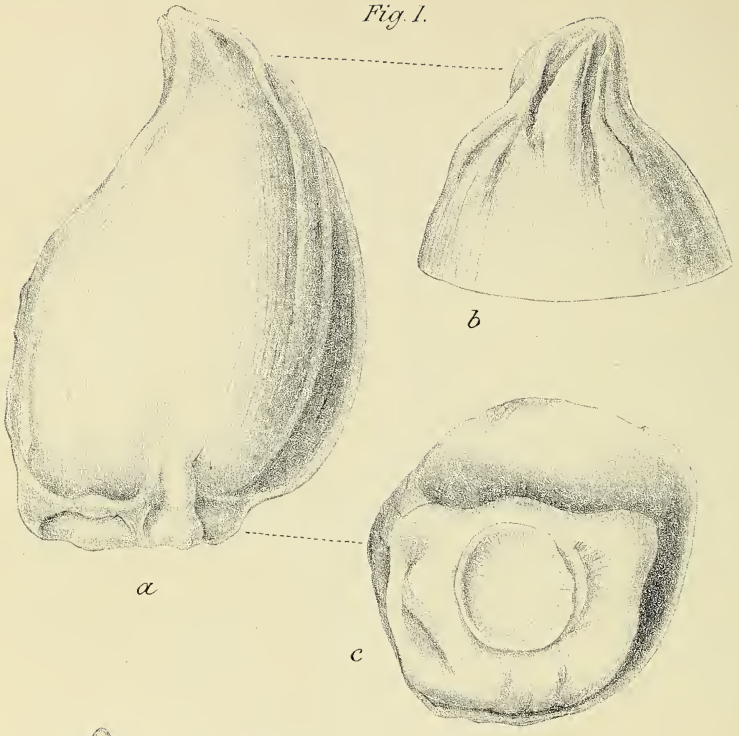
Fig. 7. Vertical section of bulb of *Allium giganteum*, Regel, received from the Royal Gardens, Kew, Nov. 19, 1888.

Fig. 8. The same after having been placed in a solution of common salt.

Fig. 9. Transverse section of the same.

The specimens from which Figs. 7, 8,and 9 were taken are now in the Museum of the Royal Gardens, Kew. All these drawings are natural size, and were done by Miss M. Smith from the originals, except Fig. 5, which was taken from a sketch made by myself.

Fig. 1.



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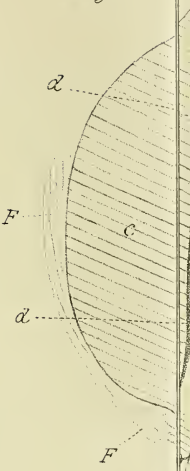

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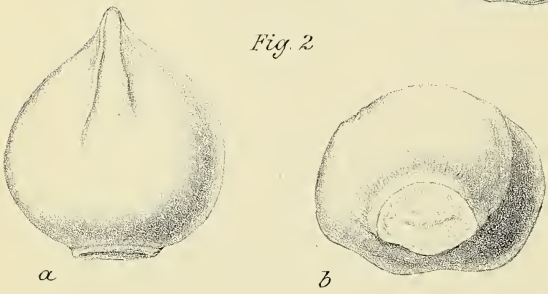

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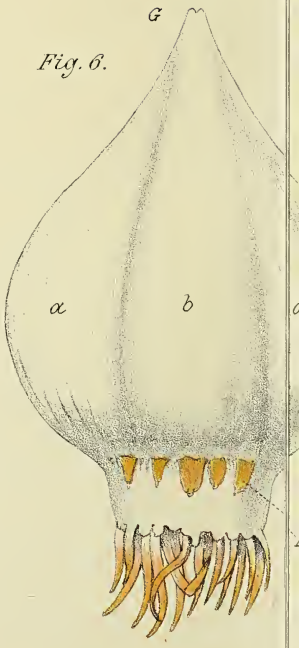
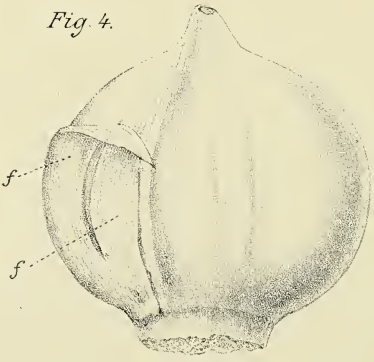


Fig. 3.

Fig. 4.



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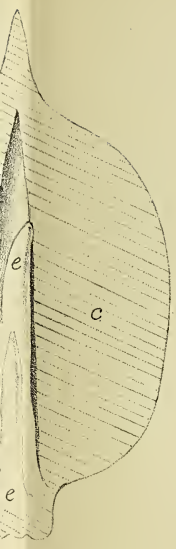

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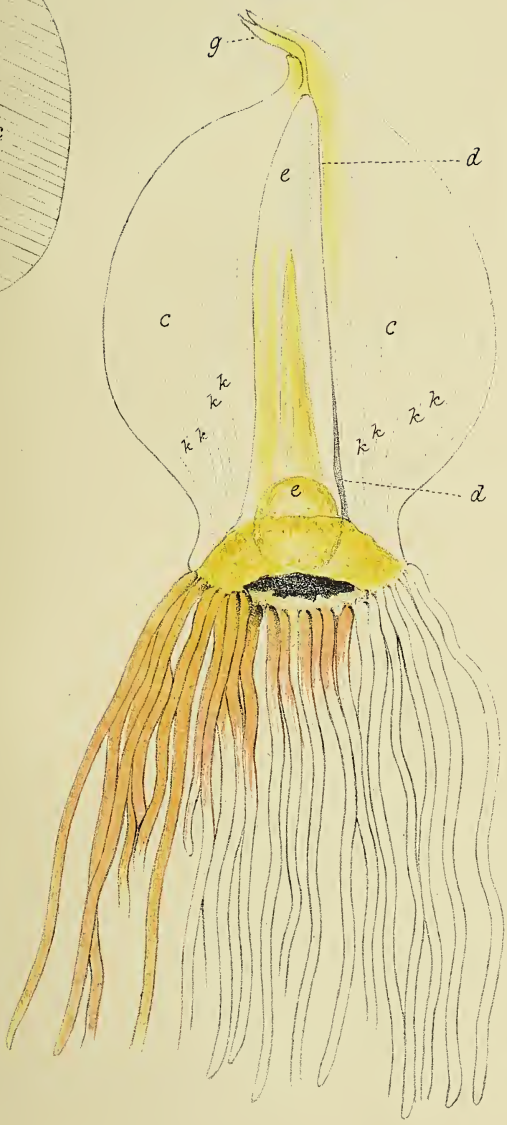

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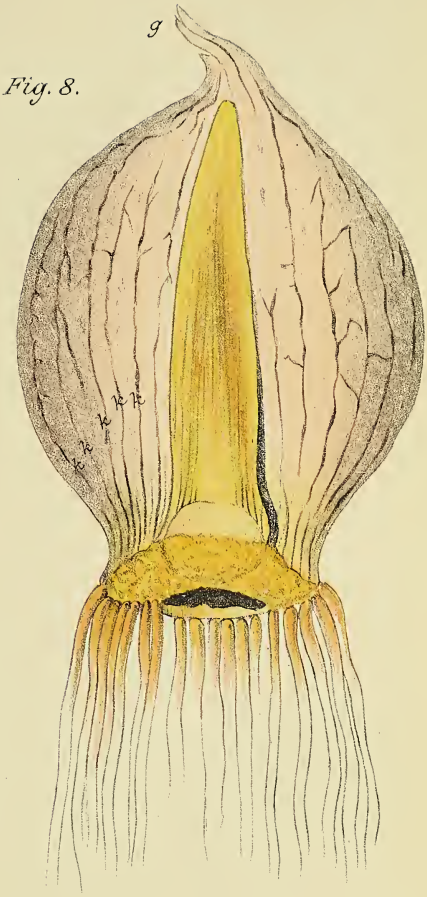

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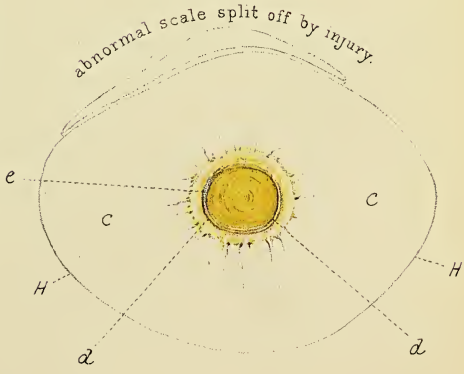

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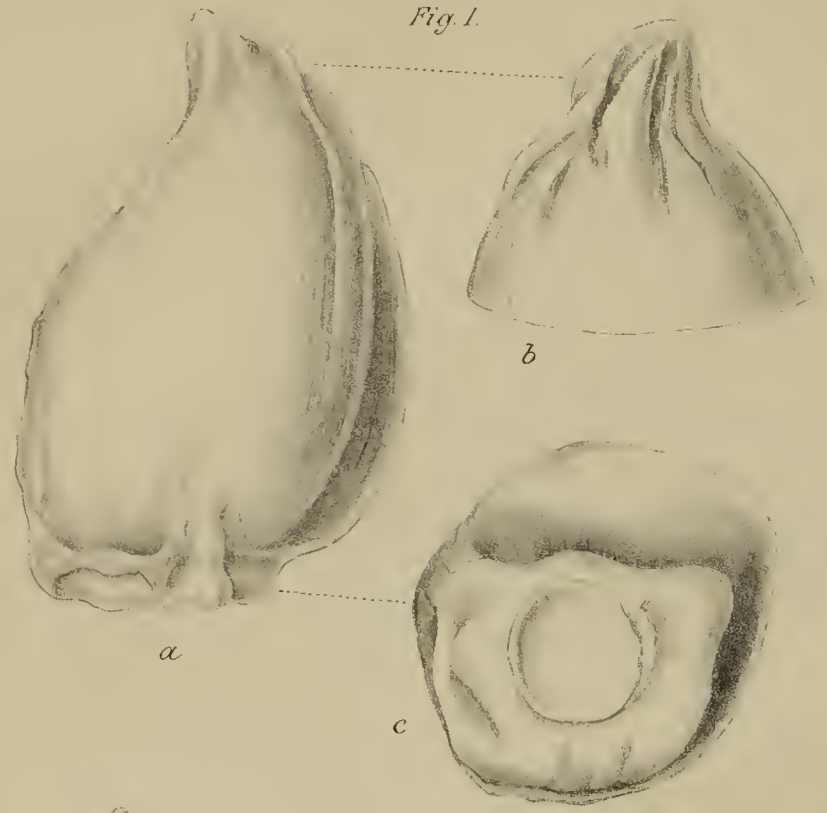
Fig. 1.



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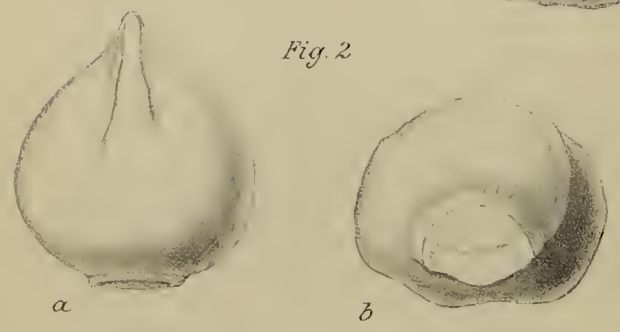
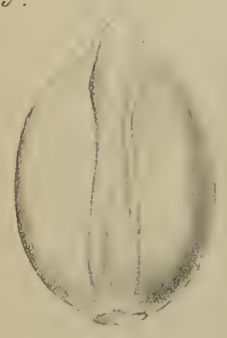


Fig. 3.



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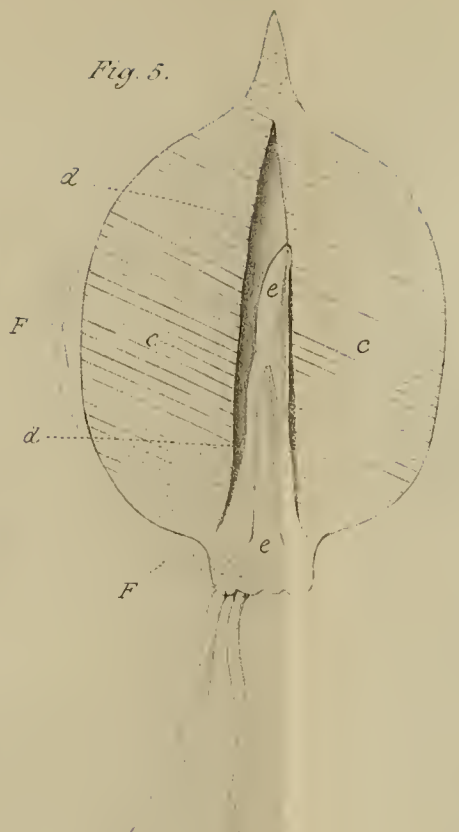

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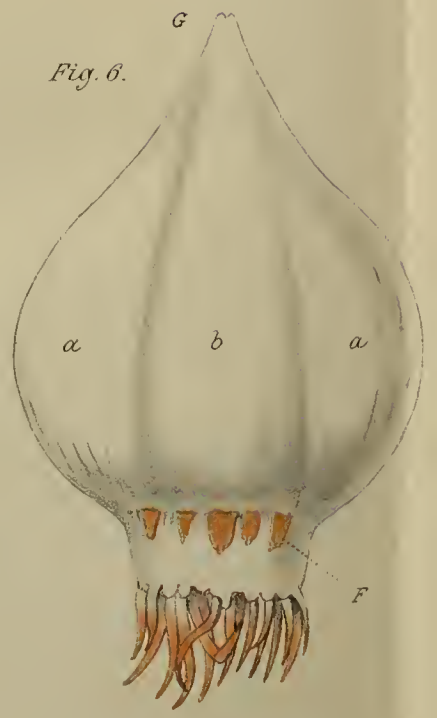

Fig. 7.

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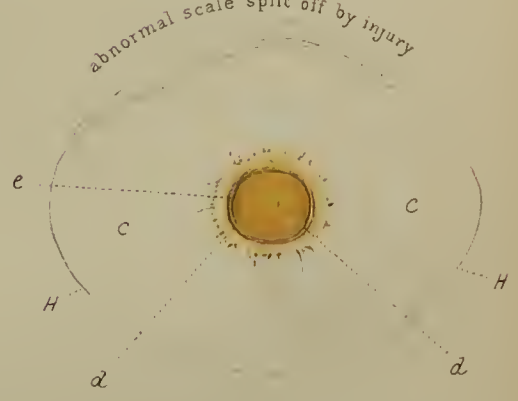


M. E. Smith del.

AITCHISON. — ON BADSHA OR ROYAL SALEP.

University Press, Oxford.

On the Function of Laticiferous Tubes.

BY

PERCY GROOM, B.A.,

Frank Smart Student, Gonville and Caius College, Cambridge.

With Plate XI.

THE nature of the functions performed by laticiferous tubes has long been the subject of keen discussion. Trécul regarded the laticiferous system as comparable with the venous system of animals. Richard, Treviranus, and Von Mohl compared it with the liver or salivary glands. Faivre [1] regards the tubes as food-reservoirs. According to Schullerus [2] and Treub [3] the tubes conduct the products of assimilation, at least in *Euphorbia*. The three last-named observers arrived at their conclusions by noting that the latex contained useful substances such as proteids, starch, sugar, etc. They then made experiments to prove that these substances were used as food by the plant. Their researches have been criticised by A. F. W. Schimper.[4] It may briefly be said that

[1] Faivre, Recherches sur la circulation et sur le rôle du latex dans le *Ficus elastica*, in Ann. des Sc. Nat. sér. 5, t. X, p. 33, 1886; Id. Études physiologiques sur le latex du mûrier blanc. Ibid. t. X, 1869; Id. in Comptes Rendus, t. LXXXVIII, 1879.

[2] Schullerus, Die physiolog. Bedeutung d. Milchsaftes von *Euphorbia Lathyris*, in Abhandl. d. bot. Vereins d. Provinz Brandenburg. XXIV, p. 26, 1882-3.

[3] Treub, in Ann. du Jardin bot. de Buitenzorg, t. III.

[4] Schimper, Ueber Bildung u. Wanderung der Kohlhydrate in den Laubblättern, in Bot. Zeit. 1885.

Annals of Botany, Vol. III. No. X. May 1889.]

their results merely show that changes do take place in the constitution of the latex. Starch, for instance, does disappear to a certain extent under the conditions of the experiments. These results may have been partly pathological, though not wholly so, because some of the changes recorded take place naturally during the life of the plant. But no proof was offered to show that the substances were used as food. Again, Hansen[1] concludes that the apparently useful ferments found in latex are useless excretions which merely happen to act as ferments. On the other hand, Van Tieghem[2] and Mdlle. Leblois[3] are of opinion that the laticiferous tubes are excretory in nature. The former goes so far as to suppose that all the constituents of latex are useless excretions. He points out that starch in the guard-cells of the stomata of fallen leaves, and the sugar in fleshy fruits, are true excretions. But in reality neither of these substances can be said in these cases to be a useless excretion. The sugar has a biological function, whilst the starch probably was manufactured for consumption. There is no evidence that starch or sugar can be degradation-products absolutely useless to the plant. Schimper[4] dismisses the theory that the sugar of extrafloral nectaries is an excretion of which the plant wishes to rid itself. As further arguments against Van Tieghem's view, we may allude to the large quantity of starch present in the latex of young Euphorbias[5]. Also we may call attention to the fact that this starch does wholly or partially disappear under normal and experimental conditions[6].

On the whole it may be stated that latex mainly consists

[1] Hansen, Ueber Fermente u. Enzyme, in Arbeit. des bot. Instit. Würzburg, Bd. III, p. 287.

[2] Van Tieghem, Second mémoire sur les canaux sécréteurs des plantes, in Ann. d. Sc. Nat. 1885. Vuillemin, Remarques sur la situation de l'appareil sécréteur des Composées, in Bullet. soc. bot. de France, Bd. VI, p. 108, 1884.

[3] Leblois, Sur le rôle du latex des Composées, Bullet. soc. bot. de France, Bd. VI, p. 122, 1884.

[4] Die Wechselbeziehungen zwischen Pflanzen und Ameisen im Tropischen Amerika. Jena. 1888.

[5] Treub, loc. cit.

[6] Schullerus, loc. cit., und Treub, loc. cit.

of substances which are usually supposed to be useless excretions[1]. Up to this point then no positive statement can be made concerning the functions of laticiferous tubes. It may be that they play different parts in different plants.

Haberlandt[2] has recently endeavoured to confirm the view that laticiferous tubes conduct carbohydrates. He observed the distribution of the tubes in leaves. He finds that the laticiferous tubes branch especially copiously beneath the palisade-cells which form essentially the chief assimilating system of the plant. Moreover, the free tubes which branch off from the vascular bundles very often direct their course upwards, and push up between the palisade-cells in order to receive the products of assimilation direct from the assimilating cells. The tubes frequently branch beneath the palisade-cells; whilst the latter often incline in small tufts towards the branches. When this mode of direct communication is not possible, funnel-shaped collecting cells are inserted between the tubes and the assimilating cells. Haberlandt also finds that the development of an extensive laticiferous system in leaves is accompanied by a corresponding diminution in the conducting parenchyma. Pirotta and Marcatili[3], are led, by numerous anatomical observations, to support Haberlandt's view.

It may however be pointed out that this supposed mode

[1] Schullerus's assumption that latex has a relatively large amount of proteids is at variance with published analyses. The microchemical methods used by Schullerus were inadequate, considering the variety of substances present. In testing for proteids he ignored the facts that sulphuric acid will give a reddish colour with other substances, with some resins, with fatty acids and sugar, etc.; iodine would colour the tannin, whilst Fehling's sugar test is unsatisfactory in the presence of dissolved proteids.

[2] G. Haberlandt, Ueber die anatomische Beziehung des Assimilationssystems zu den Milchröhren, in Sitzungsberichte der Wiener Akad., Bd. LXXXVII, 1883; Id. Physiologische Pflanzenanatomie, p. 226; Id. Ueber das Assimilationssystem, in Berichte d. deutschen bot. Gesellschaft, Bd. IV, p. 208, 1886.

[3] Pirotta e Marcatili, Sui rapporti tra i vasi laticiferi ed il sistema assimilatore nelle piante, in Annuario d. R. Instit. Bot. di Roma, Anno II, fasc. 1, p. 48; Id. Ancora sui rapporti tra i vasi laticiferi ed il sistema assimilatore nelle piante, ibid. Anno II, fasc. 2, p. 156. Marcatili, I vasi laticiferi ed il sistema assimilatore, ibid. Anno III, fasc. 1, p. 17.

of distribution of the tubes would be of equal significance were the tubes excretory organs, or nerves influencing the metabolism of the cells. Further, the argument to be drawn from the apparent correlation between the development of the system of tubes and that of the conducting nerve-parenchyma, is inconclusive, inasmuch as the nerve-parenchyma is not exclusively concerned in the conduction of carbohydrates. The nerve-parenchyma stores tannin, alkaloids, salts, etc.; hence the apparent correlation might have reference to one or other of these functions, and not at all to the conduction of carbohydrates. In fact, Van Tieghem uses this argument in support of his view that the laticiferous tubes are excretory in function. And I find that, as might be expected, the conducting parenchyma and the laticiferous tubes may both be well developed in the same leaf.

Schimper's observations on *Euphorbia* are at variance with those of Haberlandt. He found that the tubes are extensively distributed beneath the epidermis, and that they nearly always end there. By darkening leaves, he observed the mode of conduction of the carbohydrates. He showed thus that there is no reason for believing that the tubes take any share in this conduction.

The present observations were undertaken for the purpose of determining the distribution and mode of ending of the laticiferous tubes in leaves. The mode of conduction of carbohydrates was also observed, in order to decide if the tubes do assist in the process.

Whole leaves or tangential sections were observed in chloral-hydrate. In addition transverse sections were made. These latter are not so satisfactory for the purpose because of the irregular course of the tubes. Haberlandt, Pirotta, and Marcatili seem to have judged chiefly from transverse sections. I found that Haberlandt's statements were exaggerated.

To see the mode of conduction of the starch either entire plants or attached leaves were darkened. The leaves were subsequently examined after treatment with a solution of iodine in chloral-hydrate.

The following plants were investigated :—

Euphorbiaceae :—*Euphorbia Helioscopia*, *E. Peplus*, *E. Cyparissias*, *E. puniceus*, *Sapium* sp., *Manihot utilissima*, var. *dulcis*.

Papayaceae :—*Carica Papaya*, *Jacaratia* sp.

Artocarpeae :—*Pharmacosycea* sp., *Ficus elastica*, *Urostigma* sp.

Asclepiadaceae :—*Asclepias curassavica*.

Compositae :—*Hypochaeris radicata*.

Euphorbiaceae.

Euphorbia Helioscopia (Fig. 1) is admirably suited for observation because of the extreme thinness of the leaves. The whole leaf was rendered transparent by chloral-hydrate. Tracing a wide tube from the base of the leaf, it runs and branches in the spongy parenchyma. All the tubes thus formed continue their course, here and there crossing or running for a short distance with a vascular bundle, and finally pass through the palisade-layer, terminating in a copiously branched subepidermal system. Occasionally a tube again dips down into the mesophyll. In the few cases in which I observed this descent into the mesophyll, the tubes branched there, and the branches ascended once more to the epidermis. Occasionally the tubes in the mesophyll give off short blunt processes, which showed no intimate relation with the adjoining cells, but rather suggested the appearance of young branches. Some tubes, on reaching the edge of the leaf, bend inwards and may end in the mesophyll. Thus the tubes end in any part inside the leaf, but chiefly beneath the epidermis. The complicated and tortuous course of the tubes is difficult to reconcile with Haberlandt's theory of conduction by the shortest route.

The leaf of *E. Peplus* (Figs. 2, 3) is very similar to the one previously described. There is a well-developed system of subepidermal tubes beneath the lower epidermis, though that

below the upper epidermis is considerably more extensive. The tubes end in a very similar manner in *E. Cyparissias* and *E. puniceus*.

The arrangement of the tubes in the large leaves of *Sapium* sp. (Figs. 4, 5, 6), does not differ from the preceding type. The sub-epidermal system is very extensive indeed. Frequently, however, cells of the spongy parenchyma form an incomplete sheath round the tubes, as described by Haberlandt in some other leaves. In the midrib the tubes run close to the vessels or in the cortex. The cortical tubes send out branches which run below the epidermis, and spread out into the lamina.

In *Manihot utilissima*, var. *dulcis*, the laticiferous tubes accompany the vascular bundles of the leaves to a large extent. Hence the free isolated portions of the tubes are much shorter than in the preceding euphorbiaceous leaves. There is no sub-epidermal system of tubes. The most that the tubes do, is to push up between the extremely long and narrow palisade-cells.

Conduction of carbohydrates in Euphorbiaceae.—The present observations on *Euphorbia Peplus* agree precisely with those of Schimper. The carbohydrates appeared to be conducted by the nerve-parenchyma just as if there were no laticiferous system. An additional experiment was performed with these leaves. Leaves poor in starch were separated from the plant. They were then left exposed to daylight in a saucer containing water. The leaves continued to live for days and manufactured starch. They were collected in the morning, day after day, for five days. A large amount of starch was present in the leaves finally. This starch was especially collected inside or close to the nerve-parenchyma. There was no aggregation of starch in the region of the free laticiferous tubes, neither was there any appreciable difference in the quantity of starch inside the tubes. But this last fact could only be observed very incompletely and solely in the free tubes (i.e. tubes separate from the bundles), because of the large amount of starch present. These facts were the more

striking because the general parenchyma of the upper half of the leaf contained a considerable amount of starch. So, unless the conducting apparatus was disabled, it appears that it must have been overworked, and could not store or remove the starch sufficiently rapidly. Hence the assistance of any accessory storing or conducting apparatus would have been very welcome. Much stress is not laid on these observations with isolated leaves, as the conditions were abnormal. Though, as far as the tubes are concerned, mere section does not have any serious affect, in some plants at any rate[1]. The laticiferous tubes contained starch till the death of the plant.

In *Sapium* sp. the laticiferous tubes contain rod-shaped starch-grains. Owing to the large size of the leaves, quantitative statements concerning the starch inside their tubes are not to be wholly trusted. However, there was no sign of diminution of this starch in leaves darkened for forty-eight hours. The starch-grains of the general leaf-parenchyma were excessively minute in my material. In the darkened leaves starch could only be seen inside the tubes, in the nerve-parenchyma of fair-sized nerves, and in the guard-cells of the stomata. Hence the nerve-parenchyma had conducted the starch from the general leaf-parenchyma; yet considerable quantities of starch remained in the peripheral subepidermal tubes.

The Manihot-leaf is not eminently suited for the study of the question, because the free parts of the tubes are relatively short.

Artocarpeae.

The leaves of *Pharmacosycea* sp. are moderately thick. The upper epidermis is succeeded by a layer of aqueous tissue. Beneath this in turn come two layers of palisade-cells. In the spongy parenchyma the tubes, as a rule, simply cross from vascular bundle to vascular bundle, but sometimes they end in this layer. They then ascend to the palisade-layers in which they form a very complete system. Many of them

[1] See Schullerus and Faivre, loc. cit.

reach the hypodermal-layer, beneath which they run for a considerable distance, and they finally end either below or between its cells. Some tubes descend to the lower epidermis, and either end there or turn back into the mesophyll. In one case I observed a tube ending on the surface of the leaf between the cells of the lower epidermis (Fig. 8).

In *Ficus elastica* the tubes can be easily seen passing through the aqueous tissue, and ascending to the upper epidermis (see also Marcatili's figure). Their course through the aqueous layer is usually oblique.

In *Urostigma* sp. (Fig. 9) the distribution of the laticiferous tubes in the leaf is very similar to that of *Pharmacosycea*. Tubes pass through the aqueous layer and reach the epidermis.

Thus in the Artocarpeae there is no considerable subepidermal system as in *Euphorbia Peplus*. But laticiferous tubes may pass right away from the assimilating cells through the aqueous tissue.

Conduction of carbohydrates. In *Pharmacosycea* sp. carbohydrates travel along the brown tannin-containing nerve-parenchyma-cells. In a few cases the cells of the incomplete sheath investing a tube contained more starch than the adjoining cells. But this was only seen when, for some reason, the distribution of the starch of the darkened leaves was more irregular than usual.

Papayaceae.

In the leaf of *Carica Papaya* there is a considerable vascular network close beneath the palisade-layer. So the connection between the palisade-cells and the nerve-parenchyma is very intimate and direct. The laticiferous tubes form a complex anastomosing system. Most of the free tubes merely traverse the meshes of the vascular network to connect tube with tube. Branches ascend into the palisade-layer; and Pirotta and Marcatili trace some of these branches to the epidermis. There is no important subepidermal system of tubes. The tubes frequently form an incomplete sheath round the tracheides of the fine vascular bundles.

Jacaratia sp. (Fig. 7). The structure of the leaf is somewhat abnormal. The cells of the upper epidermis are large, and some invade the palisade-region. Amongst the normal palisade-cells are broader brownish cells which stain more deeply and contain more tannin. Most of the free parts of the tubes merely run from vascular bundle to vascular bundle. However, branches are sent up for a shorter or longer distance between the palisade-cells.

Conduction of carbohydrates in Papayaceae. The leaves of the Papayaceae mentioned are not well suited for studying the possible function of the laticiferous tubes, because these latter have a relatively small free course. The leaves of *Carica Papaya* were full of starch. After they had been darkened for forty-eight hours the distribution of the starch was rather irregular. However, in certain regions of the leaf the starch was confined almost solely to the nerve-parenchyma. And seeing the direct connection of the palisade-cells with these nerve-parenchyma-cells, we cannot wonder that the laticiferous tubes show no signs of participating in the process of conduction of starch.

Compositae.

In *Hypochaeris radicata* the disposition of the tubes of the leaf agreed with Haberlandt's description, in that the tubes end in the mesophyll. The tubes frequently forked close to a mesophyll-cell, exactly as Haberlandt states. I failed to discover tubes ascending to the epidermis.

Asclepiadeae.

In the leaf of *Asclepias curassavica* the tubes, after leaving the vascular bundles, run loosely through the spongy parenchyma and end there, or they end in the palisade-layers. A very few tubes reach the epidermis. Their loose and irregular course through the spongy parenchyma certainly does not suggest that the tubes are calculated to conduct plastic material by the shortest route.

CONCLUSIONS.

1. The laticiferous tubes may be distributed throughout the whole of the leaf, and may end in contact with both the epidermis and the mesophyll.

2. In some leaves the endings of the tubes are chiefly in contact with the epidermis; in others again the endings are chiefly or exclusively away from the epidermis.

3. The tubes may, in the leaves, desert the assimilating tissue altogether, as in the Artocarpeae where the tubes pass through the aqueous tissue to the epidermis.

4. Thus there is no essential connection between the endings of the laticiferous tubes and any particular tissue of the leaf. Hence we gain no definite insight into the function of the tubes by observing their mode of ending.

5. Observations on the conduction of carbohydrates in darkened leaves tend to show that the tubes do not conduct carbohydrates.

It may be pointed out that this method of observing the transport of carbohydrates is not perfectly satisfactory. It is conceivable that carbohydrates might be removed by the tubes so rapidly as not to permit the formation of transitory starch in the adjoining cells; hence it would be extremely difficult to observe that the tubes assisted in this conduction. Another fact tells us that, if carbohydrates be conducted along the tubes, conduction must be rapid; it is that carbohydrates are present in the latex in small quantities, in fact sometimes analysis fails to detect their presence at all. Here we see the value of the experiments on the euphorbiaceous leaves; in them the movement of the starch is very slow, at any rate, when the leaves are darkened. In addition the complicated and tortuous course of the tubes does not suggest rapid conduction. So altogether there is no reason for supposing that the tubes conduct carbohydrates.

What then is the function of the starch inside the tubes? It has been shown that it is improbable that the starch is a useless excretion. Yet when leaves or whole plants are darkened for a considerable period, starch remains in the tubes.

In fact, all the starch is used except that in the laticiferous tubes (sieve-tubes ?), and the guard-cells of the stomata. This suggests that the starch may have a local use inside the tube. Treub, in his cautious paper, says that his results might be thus explained, but that it is difficult to conceive of any such local use. The starch might easily, directly or indirectly, give rise to tannin,[1] resin, organic acids, etc. And recently Stahl, in his admirable work 'Pflanzen und Schnecken,' has suggested a use for some of these bodies. He conclusively proves that many substances, such as tannin, acid secretions, bitter bodies, ethereal oils, etc., protect plants from the attacks of animals. He supposes that this protective function often belongs to laticiferous tubes. This would explain the frequent approach of the tubes to the surfaces. It cannot be pretended that this is a complete explanation of the function of laticiferous tubes. It seems impossible to discover what is their function, or to ascertain if there is one function common to all laticiferous tubes, until microchemical methods are vastly improved, or until analyses of latex in its various stages are made.

I take the opportunity of thanking Prof. Schimper, at whose suggestion this work was undertaken, for his advice. He also very kindly handed over to me the material which he had collected and prepared in Brazil.

[1] For instance see observations of Briosi (quoted in Mayer's Agriculturchemie), and Schulz, in Flora, 1888, who show that tannin may replace starch. See also Hanstein in Bot. Zeit. 1868, and Dippel (quoted in Haberlandt's Anat. p. 333), with reference to resin.

EXPLANATION OF FIGURES IN PLATE XI.

Illustrating Mr. Groom's paper on the Functions of Laticiferous Tubes.

Fig. 1. From *Euphorbia Helioscopia*, showing the course of a tube from a vascular bundle, through the spongy parenchyma, and palisade-layer, up to the epidermis.

Fig. 2. From *Euphorbia Peplus*. Surface view of the upper epidermis, with a laticiferous tube beneath it. Leitz, oc. 1, obj. 7.

Fig. 3. Ditto. Lower epidermis.

Fig. 4. *Sapium* sp. Surface view of the upper epidermis, showing laticiferous tube beneath, also palisade-cells.

Fig. 5. Ditto. Longitudinal section through the midrib, showing a laticiferous tube running below the epidermis. Leitz, oc. 1, obj. 7.

Fig. 6. Ditto. Section showing blunt ending of a laticiferous tube in the palisade-layer. Leitz. oc. 1, obj. $\frac{1}{16}$.

Fig. 7. *Jacaratia* sp. Trans. section of epidermis and palisade-layer, showing a forked tube passing up into the latter. Leitz, oc. 1, obj. $\frac{1}{16}$.

Fig. 8. *Pharmacosycea* sp. Surface view showing a tube running up to the surface of the lower epidermis. A portion of the epidermis, near the end of the tube, has been cut away, and both the walls of the epidermal cells and of the tube are slightly frayed close to the gap. Leitz, oc. 1, obj. 7.

Fig. 9. *Urostigma* sp. Surface view of hypoderma, with a laticiferous tube running and ending beneath it. Leitz, oc. 1, obj. 7.

Fig. 1.

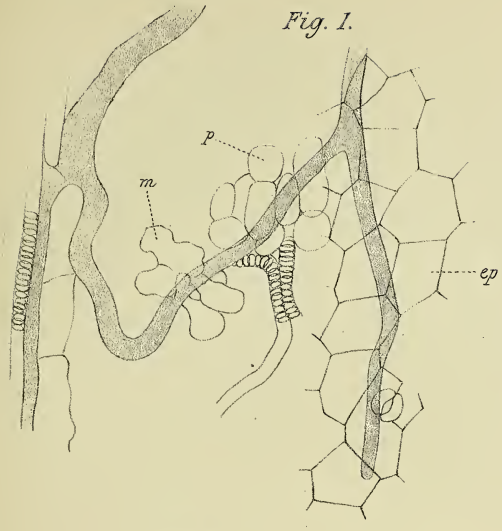
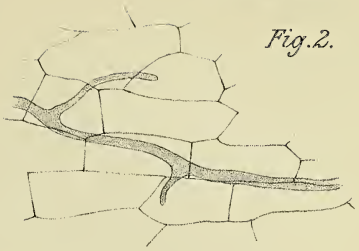


Fig. 2.



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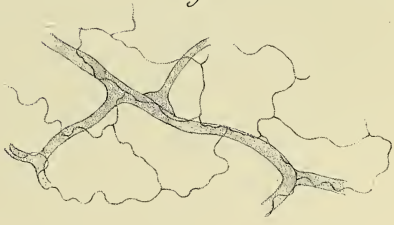

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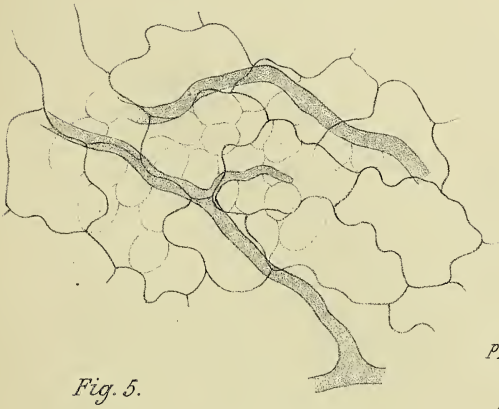

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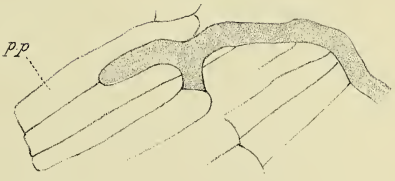

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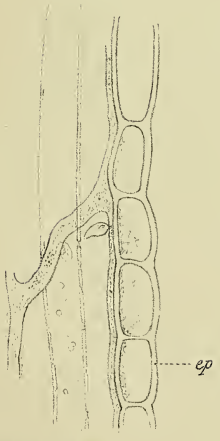

Fig. 8.

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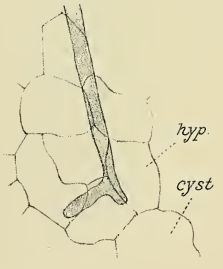


Percy Groom del.

University Press, Oxford.

GROOM.—ON FUNCTION OF LATICIFEROUS TUBES.

On the Vesicular Vessels of the Onion.

BY

A. B. RENDLE, B.A.,

Scholar of St. John's College, Cambridge, Assistant in Botany, British Museum.

With Plate XII.

HANSTEIN[1] discovered these structures in various species of Onion, and grouped them with the rows of raphide-containing sacs found in many Monocotyledons as 'vesicular-vessels' (*Schlauchgefässe*). Excepting a brief description in De Bary's Anatomy[2], mainly a *résumé* of Hanstein's results, there does not appear to be any other account of them, nor have they yet been anywhere adequately figured. The account that follows shows that these 'vesicular-vessels' are not at all well named. They are not cell-fusions, and continuity between the contents of adjacent members can very rarely be seen; hence the term 'vessel' is inapplicable, they are simple cells. I should like therefore, following a suggestion made by Dr. Vines, to replace the distinguishing name they have hitherto borne by the term 'laticiferous cells.'

Development and Distribution. Hanstein gives no account of their development beyond suggesting in a general way the difficulty of finding the primitive structures in the very young parts, and assuming by analogy with *Tradescantia*, in which he describes the development of the raphide-containing vessels,

[1] Monatsschr. Berlin. Acad. 1859, p. 705.

[2] De Bary, Comp. Anat. of Phanerog. and Ferns, Eng. edit. p. 147.

that a similar development is common to all the genera where 'vesicular-vessels' are found; i.e. that they are formed from rows of cells by absorption of the transverse walls. Investigation shows, however, that in the onion each segment originates from a single cell which is at first not very much longer than the cells of the neighbouring parenchyma, but distinguished from these by its very large oval nucleus, and by its contents staining more deeply with iodine and the aniline dyes, especially Hofmann's blue. This is well seen in tangential and radial sections of the base of an internal succulent leaf which has not yet begun to grow out (Fig. 1).

Rows of somewhat elongated cells run longitudinally, parallel to the epidermis and separated from it by usually two layers of parenchyma. The transverse septa are not yet pitted, and sections treated (after Gardiner) for several seconds with strong sulphuric acid containing methyl-violet show no signs of communication between the members of the series, through the swollen cell-walls. With the outgrowth of the leaf from the bud the cells become proportionately elongated, and the transverse walls soon assume the usual pitted appearance figured by Hanstein. In the succulent base of an elongated leaf the cells remain comparatively short, and at the extreme base are very short, and here the longitudinal series are irregularly connected, as Hanstein states, by cross unions (Fig. 6). In this succulent leaf-base they are almost invariably separated from the epidermis by two layers of parenchyma, rarely by one only; in the green tubular part of the leaf, however, they often lie a little deeper, being just below the chlorophyll-containing palisade tissue, i.e. between the more special assimilating tissue and the elongated cells containing comparatively few chlorophyll-corpuscles between which the vascular bundles run (Fig. 4). Here too the laticiferous cells are much elongated.

In the bulb-scale, as Hanstein states, two series are frequently found running alongside each other, and the wall separating them longitudinally is then also pitted; when parenchymatous cells abut on them the dividing wall is simple.

I have given a figure of the former case as none has hitherto been published (Fig. 2).

The rows of cells end bluntly at the extreme base and apex of the leaf; no sign of any connection whatever with either the vascular bundles or the assimilating tissue can be seen, nor do they follow the course of the bundles at all. We find them very early in the life of the plant. In the first leaf of the seedling, which pushes up through the soil as a pointed arch and subsequently carries the seed up in the air, a longitudinal section shows the laticiferous cells in their usual position throughout the whole length of the leaf; the transverse septa are here thin and unpitted.

Contents. As Hanstein pointed out, the cells are filled with a more or less granular turbid fluid which appears on the cut surface of an onion as a pale milk; in the green leaves the contents are clearer and more watery than in the succulent leaf-scales. I cannot find that any food-substances are present; there is no starch or sugar, though glucose is present in large quantities in the surrounding cells. Fats cannot be detected; and the ordinary microchemical proteid-tests, e.g. Millon's, and the xantho-proteic, give purely negative results, and the usual proteid-solvents, such as salt-solution (10 per cent. and saturated), 1 per cent. or 5 per cent. potash, cause no apparent diminution of the contents, if sections be watched under the microscope while running in the reagent. The action of 5 per cent. potash for nearly two hours is without apparent effect. Carbohydrate, fatty and proteid-food-stuffs are therefore presumably absent, at any rate in quantities appreciable by the existing methods of microchemistry. The contents appear to consist merely of a resinous excretion soluble in alcohol. Hanstein says that calcium-oxalate never occurs, but it can be found in the laticiferous cells as well as in the surrounding parenchyma at the base of the succulent leaf, in the form of long crystals.

Structural Changes. On first examining these cells[1], there

[1] Vines and Rendle, Proc. of Camb. Phil. Soc., 1886.

were seen on many of the transverse walls little nodules staining bright red with corallin-soda and bright blue with Hofmann's blue; in fact reacting exactly like the callus of sieve-tubes and evidently consisting of the same substance. As this was first noticed in a resting onion, it seemed probable that, like sieve-tubes, the cells were only actively functional during vigorous growth and closed in seasons of rest. Resting onions were accordingly germinated, but the callus did not disappear, a result to be expected, since the succulent leaves being merely food-reservoirs do not return to active life, but are gradually used up as the shoot grows out. I have since carefully examined a great many specimens in different stages from young seedlings upwards, with the following results.

In the first green leaf of the seedling the elongated cells contain no callus, but their transverse septa are thin and unpitted. In the green leaf of a seedling only $6\frac{1}{2}$ inches long little nodules of callus are present on the transverse septa, chiefly at the corners where they join the side walls; this was found in about three-fifths of the individuals examined of vigorously growing seedlings in warm sunny weather at the beginning of June.

Examination of the parts of an ordinary small spring-onion, e.g. one with two green leaves and a bulb of about half-an-inch maximum diameter, shows the following distribution of callus-formation:—

1. *Succulent base of external green leaf.* Callus frequent and extensive on all the transverse septa and occasionally on the side walls; the cells well filled with the latex (Fig. 3).

2. *Succulent base of next internal green leaf.* Nodules of callus found on the majority of the transverse walls, but less in quantity than in 1.

3. *Unelongated leaf enclosed by* 1 *and* 2. Just green at the tip. No trace of callus in the cells, which are still very small. In a similar leaf from another similar onion there was a very partial callus on about half the number of transverse septa examined (Fig. 2), but the leaf enclosed within this and about half an inch long showed no callus at all, the

cells being of course in an extremely young state and very short.

4. *Portion of leaf between the succulent base and the green tubular part.* The very elongated cells show nodules of callus on the transverse septa.

5. *Piece of green tubular leaf* just above the colorless sheathing part. Small callus-formations on almost all the transverse septa examined and occasionally on the side walls (Fig. 4). The next younger tubular leaf, about a quarter-inch below the apex, shows similar small callus-plugs on several of the transverse septa examined, though not on all.

In the succulent leaf-scales of a resting onion there was callus on nearly all the transverse septa examined, and occasionally on the side walls; but in the shoot enclosed in the centre, where the tissue is of course very young, there was none on the thin unpitted transverse septa. If, however, the onion is set to germinate, the leaves of the shoot which grows out soon show a formation of callus, which is also found, just as before, in the cells of the succulent sheath-scales.

From these observations it is evident that, except in the youngest stages, and even before the transverse septa become conspicuously pitted, callus-formation occurs upon them; at first usually as small plugs, afterwards often of a more irregular form and sometimes spreading more or less over the whole plate. The complete covering of both sides, such as obtains in sieve-tubes during winter, is very rarely seen, one instance is noticed in Fig. 3, *b*.

I have repeatedly tested sections from the different parts of leaves of all the ages and in all the conditions mentioned above, to see if the pits in the walls were ever perforated, using for the purpose (after Gardiner) concentrated sulphuric acid in which methyl-violet was dissolved; or chlorzinc-iodine followed by staining with picro-Hoffmann's blue. The only cases in which perforation was observed occurred in the succulent leaf-scales of a spring-onion in which tangential sections from the lower half of the leaves showed the contents to be continuous through the swollen pits of the transverse

septa, which were apparently free or almost free from callus. Where this continuity was noticeable it was so obvious (Fig. 5) that its apparent absence in the great majority of cases is probably due, not to difficulty of observation, but to the actual fact of its absence. In the external succulent leaf of the shoot in the centre of a spring-onion, where small nodules of callus were found on about half the transverse-septa examined,—that is, where its formation was only just commencing, and where therefore, if anywhere, demonstration of continuity should be possible,—no indication of such could be found (cf. Fig. 6). The same was the case in very young stages where neither callus or pitting was visible. Not infrequently in sections where no continuity of the contents of the vesicular cells was indicated, protoplasmic continuity between the parenchymatous cells was very well shown.

In the green leaves pitting is less conspicuous and perforation could never be made out.

De Bary says the pits are not perforated, and from the present observations this would seem to be the case in the great majority of instances. At any rate, we cannot trace any direct relation between their perforation or closure and the activity of the vital processes in the plant, such as obtains with sieve-tubes. All that can be said is, that in the succulent basal leaves of young onions, in the lower half only of which perforations were observed, continuity between the contents of adjacent members of the series sometimes occurs; and it is here that our cells are most numerous and closest together, and that the longitudinal series are connected by cross-unions. The degree of protoplasmic continuity is evidently altogether insufficient to justify the application of the term 'vessel' to these structures. It is in fact no more extensive than that obtaining between parenchymatous cells.

It is interesting from this point of view that callus-formation occurs where there is no evident pitting. Thus, in a young leaf of the shoot of an old onion which had germinated, out of six transverse walls examined, five showed no trace of callus, but the sixth, which was not pitted and scarcely thicker

than the thin side wall, stained like callus, though somewhat faintly, for about a third of its length in its central portion, while just at the end of the stained part a very small more brightly staining blunt peg projected into the cell on one side (Fig. 7).

This and similar cases are of interest as regards the question whether callus is formed from the cell wall or secreted directly by the protoplasm. With regard to the participation of the wall in the formation of callus the following differences were noticed :—

1. The wall itself is not changed, but the callus is superposed sometimes only on one (Fig. 3, *a*; and 2, α), sometimes correspondingly on both sides (Fig. 3, *c*, *d*; and 2, β).

2. The wall gives the callus-reaction, but more faintly than the superposed formation, and it can by virtue of this be traced through the callus masses where these correspond in position on both sides of the plate (Fig. 3, *a*, *b*, *d*).

3. The wall cannot be distinguished at all; the staining is of a uniform tint throughout (Fig. 3, *b*, *c*).

The first case is more frequent where there is only a small callus-formation; either the second or the third usually obtains where the callus is more extensive, but sometimes where only very partial. With very extensive callus-formations, the side walls sometimes stain for a little distance beyond the transverse septum, the colour of the stain becoming fainter and fainter and gradually passing into the ordinary non-staining cellulose (Fig. 3, *b*, lower plate). These facts point to a change induced in the cellulose of the wall by which it becomes more (as in 3) or less (as in 2) converted into callus, as indicated by more or less deep staining, while pure callus is deposited on this by the protoplasm in the same way as thickening on a wall.

Function. As stated above, these laticiferous cells contain none of the ordinary food-stuffs in any perceptible quantity, nor have they any connection with the assimilating parenchyma on the one hand, or with the vascular bundles on the other. There seems to be no direct relation between presence

of callus on the walls and the general vigour of the life of the plant or its members. The resemblance to sieve-tubes is simply structural; and it may be noticed that these members of the vascular bundles of the onion are by no means few or feebly developed, so as to necessitate any additional means of transport for nutrient substances. These vesicular cells are evidently merely rows of excretory sacs which begin to be sealed up by callus very early, the smaller amount of callus in the green leaves corresponding with the less evident pitting found there. This view of their function is confirmed by the following observation. In the germination of a resting onion which had produced a vigorous shoot a foot high, and in which the formerly succulent leaves were being used up from the outside inwards, the vesicular cells in the now quite membranous scales were still crowded with the resinous latex, and became marked out as pink lines in the leaf on placing pieces in dilute alcanna-tincture. The transverse septa were still callosed, while the nuclei had almost completely broken down. Thus, at a time when the tissue had been so drawn upon to supply the growing shoot, as to reduce the leaf to the consistency of thin paper and to render it quite transparent, these laticiferous cells were still full of what must I think be therefore regarded as a purely excretory substance, one, that is, of no further use to the plant as a food-stuff. No other excretory structures are found in the tissues of the stem and leaves of the onion. Doubtless the resinous latex is of some use in the life of the plant, perhaps making it unpalatable to certain animals, or keeping them off by the peculiar smell. This smell is due to some substance which gives rise to allyl-sulphide when an onion is analysed, and which is probably contained in the latex, since a silver coin is slightly blackened thereby; but, though I have tried a great number of micro-chemical tests, I have never succeeded in demonstrating that this compound is localised. It is probably only present in small quantities, the detection of which is made practically impossible by the presence of so much resinous substance, for resins greatly interfere with the tests.

EXPLANATION OF FIGURES IN PLATE XII.

Illustrating Mr. Rendle's paper on the Vesicular Vessels of the Onion.

N.B.—In the case of sections mounted in corallin-soda the depth of stain of the callus is represented by the degree of shading. The letters D, F, refer to Zeiss' objectives: 2, to his eye-piece.

Fig. 1. Longitudinal section of the base of a young internal leaf of a spring-onion. *a*, row of young vessels; *e*, epidermis. The section had been treated with haematoxylin, and the contents of the vessels had stained deeply. D, 2.

Fig. 2. Tangential section of an internal succulent leaf of a spring-onion. The leaf had not begun to elongate. Mounted in corallin-soda to show the callus, which is very scanty. D, 2.

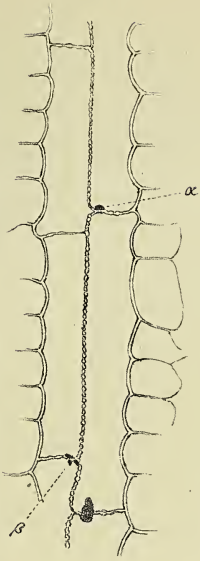
Fig. 3. From tangential sections of the base of the outside leaf of a spring-onion with two green leaves and a bulb of half-an-inch maximum diameter. Mounted in corallin-soda. Shows the callus-formation on the transverse septa and occasionally the side walls of the vessels. *a*, *b*, D, 2; *c*, *d*, F, 2.

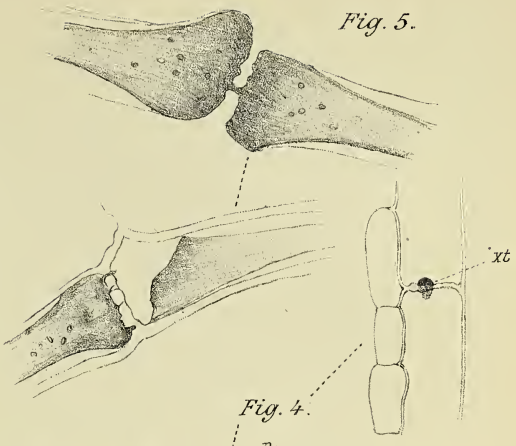
Fig. 4. Longitudinal section of a piece of a green tubular leaf just above the colorless sheathing part. Mounted in corallin-soda. *a*, vesicular vessel; *e*, epidermis with very thick and cuticularised outer walls; *p*, chlorophyll-containing parenchyma; *t*, shows a transverse septum with a callus-stopper. Mounted in corallin-soda. D, 2.

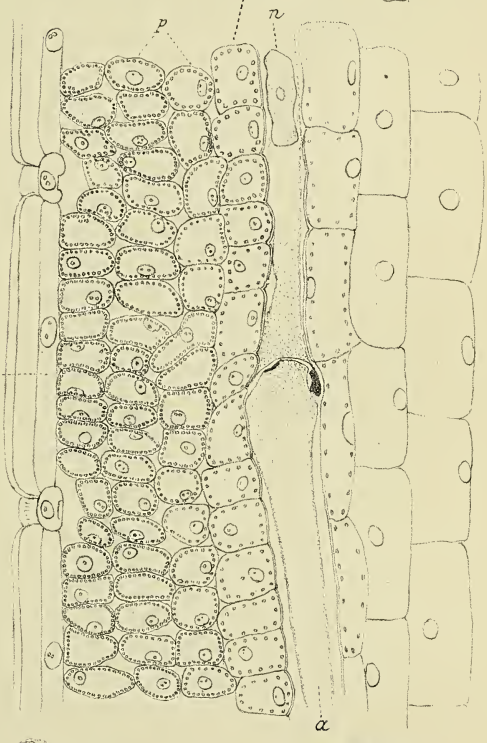
Fig. 5. From tangential sections of the base of an outside succulent leaf of a spring-onion treated with chlorzinc-iodine for twenty-four hours, and then, after thorough washing, with picro-Hofmann's blue for twenty hours. Examined in water after again thoroughly washing. The contents of the vessels can be seen passing through the pits in the swollen transverse septa. F, 2.

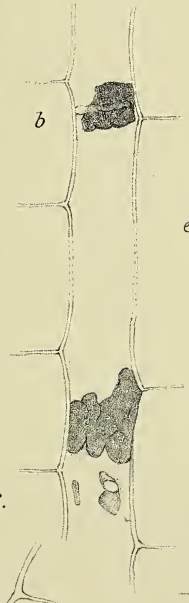
Fig. 6. Tangential section of an unelongated leaf of the shoot in the centre of a spring-onion treated for a few seconds with sulphuric acid and methyl-violet, and then thoroughly washed. No sign of connection between the deeply-stained contents of the young vessels. Shows cross-unions between two rows of vessels. D, 2.

Fig. 7. Transverse septum from a young leaf of the shoot enclosed in a germinating onion. Mounted in corallin-soda. Shows partial staining of the wall with the dye, and also a little brightly staining knob to the right of this. F, 2.









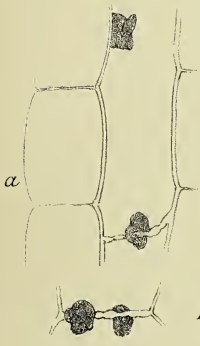


Fig. 3.

Fig. 7.

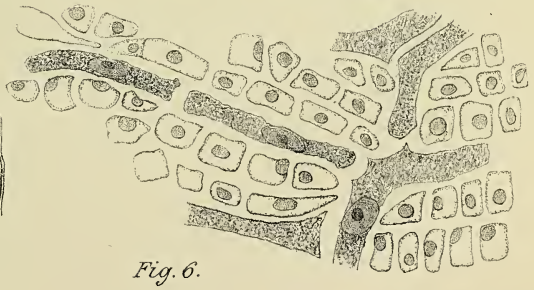


Fig. 6.

A. B. Rendle del. University Press, Oxford

RENDLE.— ON VESICULAR VESSELS OF THE ONION.

The Nursing of the Embryo and some other points in Myzodendron punctulatum, Banks et Sol.

BY

T. JOHNSON, B.Sc. (London),

University Scholar in Botany, Demonstrator of Botany in Normal School of Science, Kensington.

With Plates XIII and XIV.

MYZODENDRON PUNCTULATUM, the subject of the present paper, is the only species of *Gymnophyton*, one of the two sub-genera founded by Sir J. D. Hooker in his monograph[1] on *Myzodendron*. Though the genus is so fully described and illustrated, the appearance of several papers bearing on parasitic Phanerogams (more especially those of Treub), since the date, 1840, of the publication of the Monograph, suggested to me that a re-examination of the plant in the light of recent investigations might prove of interest. I was able to carry out this idea through the kindness of Mr. J. R. Jackson, F.L.S., Curator of the Museums in the Royal Gardens, Kew. I am much indebted to him for excellent spirit-material taken from a fine fruiting specimen collected by the 'Challenger Expedition' in Patagonia.

For convenience of ready reference the description of *My-*

[1] J. D. Hooker, Fl. Antarct. II. Plates 102–107 ter.

[Annals of Botany, Vol. III. No. X, May 1889.]

zodendron in Bentham and Hooker's Genera Plantarum[1] is inserted :—

Tribe II. Osyrideae.

Myzodendron, Banks et Sol.; DC. Prod. iv. 285; Mem. Loranth. t. 11, 12 (errore *Misodendron*) Flores dioici. Perianthium in flore ♂ 0. Stamina 2–4, circa discum parvum glanduliformem affixa, filamentis crassiuscule filiformibus; antherae terminales, erectae, ovoideae v. globosae, uniloculares, vertice 2-valvatim dehiscentes. Perianthium floris ♀ ovario adnatum, margine supra ovarium libero brevissimo, extus angulis 3 longitudinalibus interdum in alam dilatatis et inter angulos rimis totidem setam unicam pluresve foventibus instructum. Staminodia 0. Ovarium inferum, disco vix conspicuo coronatum; stylus brevis, crassus, stigmatibus 3 brevibus; ovula 3, ab apice placentae centralis crassiusculae pendula. Fructus parvus, nuceus v. utriculosus, extus setis lateralibus valde elongatis plumosis instructus v. rarius nudus. Semen conforme; embryo in centro albuminis carnosi teres, radicula supera crassa ex albumine prominula cotyledonibus minimis v. vix distinctis multo longiore.—Suffrutices ramosissimi, in arboribus parasitici. Folia alterna parva v. 0. Flores minuti, secus ramos alterni ebracteati v. in spiculas parvas amentiformes dispositi.

Species 4, Chili australis et terrae Magellanicae incolae, . . Genus habitu et embryonis radicula ad apicem albuminis prominula Loranthaceis accedit, ovarium caeterique characteres tamen potius Santalacearum.

Vegetative Organs.

The surface of the stem of *M. punctulatum* is covered by innumerable swellings, visible to the naked eye (Fig. 1). Each swelling consists of cortical parenchyma overlaid by a well-developed epidermis. At the tip of each swelling there is a stoma of peculiar form. The air-chamber is very large, contributing considerably to the size of the swelling. Though the

[1] Bentham and J. D. Hooker, Genera Plantarum, vol. iii (1883), p. 229.

stoma itself is elevated, the guard-cells are not flush with the surface, but are depressed and covered by a very thick cuticularised layer. A look at Fig. 2 will show that it is difficult to say whether the outer and inner thickening ridges belong to the guard-cells or not. The latter lie with their long axes parallel to that of the stem, and consequently are seen in section, only in cross sections of the stem. The formation of these swellings on the stem, foliage-leaves being absent, increases the assimilative surface of the stem—much in the same way as the grooved surface of the stem does in *Equisetum*—and is one of the chief distinguishing features of the sub-genus *Gymnophyton*, as contrasted with *Eumyzodendron*.

The internal structure of the stem is to a great degree explicable by a knowledge of the habit of the plant. I would refer readers to the Flora Antarctica, reminding them that it was not until nearly twenty years later than the time of publication of that work, that the nature of sieve-tubes was at all understood. *M. punctulatum* stands out horizontally from the stem of the beech, resulting in a one-sided development of its wood (Fig. 3). The pith and the greater part of the primary medullary rays consist of woody prosenchymatous fibres, containing starch. There is in the stem of *Myzodendron* the same lignification of the pith as occurs in the pith of the adventitious roots of *Hedera Helix*. Secondary thickening, by the activity of a normal cambium ring, the cells of which are of the typical form, occurs as in Dicotyledons generally. The activity is, however, confined chiefly to the formation of secondary xylem, in which secondary medullary rays, very small and inconspicuous, occur. Annual rings too are evident, though, possibly owing to the absence of foliage-leaves, and of much secondary phloem, they are not well marked. In the secondary phloem there are no sclerenchyma fibres. These form an incomplete irregular zone, lying half-way between the vascular tissue and the epidermis (Fig. 3 *s*). The sieve-tubes are very narrow, have simple oblique terminal sieve-plates, facing the radial plane, and are peculiar in being nucleated. Treatment with Fehling's solution shows that the sieve-elements

contain a great deal of sugar. Owing to the parasitism of *M. punctulatum*, the function of the sieve-tubes is very probably different from that in independent plants. The formation of proteids from carbohydrates, sulphates, and nitrates in the non-nucleated sieve-tubes of these plants is not required of the sieve-tubes of *Myzodendron*, which is supplied by its host with proteids ready-made. Its nucleated sieve-tubes are probably active, mainly, in the formation of sugar for the thickening of the xylem vessel walls, etc. It would be of considerable value to have a comparative knowledge of sieve-tubes in parasites, in their bearing on this particular point.

In the whole vascular tissue of the stem there is a diagrammatic regularity of arrangement of the parts, the relation of the secondary tissue to the cambium being very clear. In a stem $\frac{1}{3}$ inch in diameter the position of the groups of primary phloem is still marked, partly owing to the production of secondary phloem on their inner side being greater than elsewhere, and partly owing to their crushed condition. Periderm is formed from the superficial layer of cortex, lenticels are present and, in keeping with the horizontal position of the stem, are, as pointed out in the Flora Antarctica, more numerous on the under side. No clearer example of the beginning of the formation of periderm beneath stomata in stems could be desired than that of *M. punctulatum*. My first impression was that the periderm was localised, confined to the region of the stomata, cutting them off as they became functionless, but not extending further so as to form a complete zone since the secondary thickening was slight and slow. The branching of *M. punctulatum* is sympodial. Each branch elongates by apical growth for one year only; a twig at the end of its first year's growth is one to two inches long, and bears nine to twelve spirally arranged scale-leaves with relatively long internodes. The punctum vegetationis, which is usually a little awry, consists of a blunt axis ensheathed in several closely-packed leaves. So far as further growth is concerned this punctum vegetationis is barren, its meristematic tissue being dead and

leaf-axils empty. (A similar sterility is exhibited by the apex of the amentum, Fig. 1). In the axil of each of the separated scale-leaves of the twig a bud is formed; one or more of the uppermost buds of the twig are vegetative, the rest floral. In the following year the buds develop, the floral ones become female amenta which fall off at the end of the season, the vegetative ones become twigs of the current year and repeat the structure just described. As one, two, or three vegetative buds may develop into permanent branches, the result is a simple sympodium, a false dichotomy or a false trichotomy. The clustered habit, like that of *Viscum album*, is in this and the same way accounted for. The current year twig thus bears axillary buds only, the mature flowers and fruits are not formed till the second year,—a course of events which, as well as the mode of branching, is of special interest by comparison with similar phenomena in genera of the *Loranthaceae*. The buds, floral and vegetative, are peculiar, in that each one is almost completely covered in by a sheath derived from the stem and consisting of two cellular lamellae, of which the lower is much the smaller. The cells of the sheath, three or four layers thick, lose their contents for the most part, and acquire suberised walls. The bud appears at first sight to have an endogenous origin. Eichler mentions the occurrence of endogenous buds in the *Psittacanthus* group[1] of the *Loranthaceae*. The scale-leaves of the first year fall off at the end of that year, leaving a small scar; the bud, naked on expansion in the second year, pushes the two lips of the cellular sheath apart or causes them to fall off. In a three-year-old stem a small patch of periderm indicates the position of the fallen scale-leaf of the first year, and of the female amentum fallen in the second year. Slight complications may arise occasionally by the unfolding in the third or later years of a dormant vegetative or floral bud.

[1] Eichler, Blüthendiagramme, p. 551. 'A remarkable fact must herewith [*Psittacanthus* group] be noted: in most species of this group the inflorescences, although in the axils of the leaves, are of *endogenous* origin, breaking mechanically through the covering tissue, and then remaining surrounded by the same at the base in the form of a short, irregularly-lobed sheath.'

The Male Flower.

The material at my disposal contained no male flowers. They are described, with illustrations, in the Flora Antarctica [1].

The Female Flower.

The gynaeceum of *M. punctulatum* is essentially similar to that of other Santalaceous genera in that the ovary is inferior, unilocular, and contains a central placenta on which are three pendulous ovules. The floor of the ovary is depressed, forming three pouches, one for each ovule, so pronounced that several transverse sections of a flower may be made in each of which the ovary will appear trilocular. The placenta is short and occupies only the upper third of the flower, to which region the ovarian cavity also is limited (Fig. 4). Further the placenta is, practically, not free (Fig. 4). Its long pointed conical apex fits closely to the ovary-wall, just as closely as does the base of the seta of a moss sporogonium to the surface of the vaginula of a moss-plant. This, at first sight, trivial distinction is of considerable importance in reality, the condition is only one step short of that found on the one hand in many *Loranthaceae,* and on the other in many *Balanophoraceae.* In those genera, of these two orders, in which a central papilla is present, this is at first quite free; later, in most cases, in contact with the surface of the ovary as in *Myzodendron,* and in the end fused with the ovary wall so as to form with it a solid mass of tissue [2]. The ovules are pendulous from the placenta at a point equally distant from its apex and its base. Each one is slightly bent on itself, and may be described as semi-anatropous or semi-campylotropous (Fig. 5). Owing to the peculiar shape of the embryo-sac which is that of a retort, the result, so far as the position of the radicle of the future embryo is concerned, is the same as if the ovule were an anatropous pendulous one.

The ovule, just visible to the naked eye, is not, as is sup-

[1] J. D. Hooker, op. cit. p. 291.
[2] Eichler, Blüthendiagramme, p. 545.

posed, naked, but is partially covered by a single integument, formed of a single layer of large cells, leaving the apical part of the ovule naked, in which region the single layer of nucellus cells covering the embryo-sac is for the most part shrivelled (Fig. 7). The cells in the immediate neighbourhood of the egg-apparatus are well developed, and are very easily mistaken for the first endosperm cells of a young seed. I was not able to find any young ovules, and saw the embryo-sac in its mature condition only when ready for fertilisation. At this stage its cavity is full of granular protoplasm, in which the egg-apparatus and secondary nucleus are as in typical angiosperms. The antipodal cells, which were often not seen, possibly by reason of the granularity of the general contents and narrowness of the embryo-sac, appeared to vary in position, being sometimes at the end of the narrow part of the sac, at other times in the general body of the sac. The trigonous sessile flower is characterised by the presence at each of its three angles of a pair of longitudinal cellular lamellae, which form a groove, extending from near the apex to the base of the flower and enclosing a filamentous barbed appendage which has received amongst other names that of 'seta.' The surface of the groove is formed by a true epidermis, for on it are numerous simple stomata. The nature of the seta has such an important bearing on the right understanding of the homologies of the flower that I have placed before readers the following description of them from the Flora Antarctica[1]. 'The seta ascends from the base of the ovarium, and gradually elongating finally escapes from the cavity where it was lodged (Plate CIV. Fig. 10). . . . The plumose pappi of the achenium [the setae of the flower] afford one of the great peculiarities of this genus; of their function there can be no doubt, though their origin and true nature are not quite so evident. De Candolle, from an examination of very imperfect specimens, described them sufficiently accurately as scales contained in the walls of the pericarp. Guillemin

[1] J. D. Hooker, Fl. Antarct. p. 292.

also considers them to be pappiform appendices contained in fissures of the achenia. Neither of these authors offers any explanation of their true nature. Poeppig describes several species, and trusting more to a theoretical opinion of their origin than to a careful analysis of the parts, or of the definitions of De Candolle and Guillemin, he misapprehends the structure of the ovarium, considering it to be a compound body, made up of three carpels combined, and of the plumose filaments which are described in the generic character as Setae hypogynae, alternating with the ovaria, and in the observations on the genus are doubtfully called staminodia. Lastly, Endlicher regards the single ovarium as compounded of six, enclosed in a three-parted involucre, three of them fertile and three sterile, the latter being the plumose filaments.

The female flower of *Myzodendron*, consisting of a solitary ovarium, enclosed in the adherent tube of the calyx, it is evident that the plumose setae must be a production of the calyx or ovarium. The setae of *Myzodendron* contain no spiral vessels, and the true nerves of the calyx, though very obscure, may be traced in some of the species as in *M. brachystachyum*, where they appear alternating with the position of the setae. [The vascular bundles here described as true nerves of the calyx curve into the three stylar lobes (Fig. 4, *c*), and leave the 'calyx-tube' quite evascular] . . . The tissue of which these setae are composed is identical with what forms the sarcocarp of *Tupeia* and *Viscum*, namely elongated cells of great tenuity filled with a glutinous matter. . . . The elaboration of these setae, from cellular tissue, cannot be regarded otherwise than a very singular phenomenon, and as far as my observations serve it appears that it is merely a result of a rapid elongation of cellular tissue. The viscid substance, then, in this genus, instead of surrounding the endocarp, is confined within three fissures, and there collected into a terete or compressed body, which, escaping from its confinement, rapidly elongates from the growth of the cells which compose it, more than from the addition of new

matter. The plumose appearance is caused by the separation of some of the utricles which diverge on all sides in the species in which the setae are terete or in their opposite margins when the latter are compressed.'

My own observation has led me to believe the setae to be very definite structures which must be given an important place in a description of the morphology of the flower. Entering each seta at its base, and reaching to near its free apex, is a single central vascular bundle of which the protoxylem is the more marked part (Figs. 4 and 8). The rest of the seta consists of parenchymatous tissue, covered by a definite meristematic epidermis, from which at irregular intervals long upright hairs (trichomes) grow out, and stand parallel to one another, with their free tips reaching to the top of the groove in which the seta occurs. Small and hidden in the flower (Fig. 4) the seta in the mature fruit is very conspicuous, and gives the fruit a characteristic appearance (Figs. 1, 9, *b*). A longitudinal section of the elongated seta shows the elements of the vascular bundle much drawn out, especially in the upper part of the seta. I made a number of experiments to test the presence of viscidity in the seta and its hairs. The free ends of the hairs (Fig. 10) were the only parts which, before treatment, appeared to be viscid, but in no part of the seta or its hairs was I able to find viscidity, a conclusion reluctantly come to and one with which I am not satisfied. The experiments I am about to detail were accompanied by control ones on fresh viscid matter. As the material of *Myzodendron* had been in spirit since 1882 the more important of the control experiments were also made on the mucilage sacs of the roots of *Angiopteris*, material of which had been in spirit as long as *Myzodendron*. The possibility that the absence of a trace of viscidity in the *Myzodendron* seta might be due to the action of the spirit was found, judging from *Angiopteris*, to be groundless. Each seta-hair is an independent cell, with a nucleus and very much cell-sap, cut off from the epidermis and not like a root-hair, an outgrown epidermal cell. The whole hair is

protected by a well-developed cuticle, which is raised into numberless small undulating parallel ridges running lengthwise, more developed towards the tip of the hair, which is slightly bent and enlarged, and shows beneath the cuticle a thick stratified layer which looked like, but did not give, the reactions of viscid matter (Fig. 10). All the following reactions were obtained on setae of ripe fruits:—

1. A seta was examined in pure glycerine and measured at its tip. The glycerine was removed and water run in. The hairs, collapsed by the removal of the cell-sap, by being placed in spirit, filled out to a certain extent through the entrance of water, but there was no swelling of the substance of the hair. Two setae were taken from the same fruit, one placed in pure glycerine, the other in water for a day and night; there was no appreciable difference in the hairs of the two on examination.

2. Corallin-soda solution had no effect after twenty-four hours immersion of seta.

3. Methylene-blue, 50 per cent. spirit solution, for sixty hours had no effect on wall, stained the protoplasmic lining of the hairs.

Hoffman's blue had no effect.

4. Caustic-potash solution—no effect, for some time.

5. Iodine solution—tip of hair like its base orange-red, rest of hair yellowish-brown.

6. Schulze's solution—same as 5.

7. Iodine solution and sulphuric acid—the hair yellowish-brown generally.

8. Sulphuric acid—the hair, tip included, resisted the action of this reagent.

Experiments 1–4 tend to prove that viscidity is absent from any part of seta or hairs; 5–8 that the wall of the hair is formed externally of a thick cuticle, and that the tip of the hair has a thick cuticularised layer.

The vascular system of the flower is very simple. A single vascular bundle enters each sessile flower and gives off three vascular bundles, one to each seta, and, at a *little higher* point,

three other vascular bundles, one to each carpel, the carpels alternating with the setae. The setae are distinctly hypogynous and free, but protected at first by the lamellar outgrowths of the floral wall, as stamens are by the perianth in a floral bud. I propose to defer any attempt to assign to the setae their morphological value. The 'calyx-tube,' forming an epigynous sheath surrounding the base of the style, is, as has been said, evascular. On its inner surface are simple stomata like those found in the grooves on the outer surface of the flower. These stomata are few, occur at the same level and at the bottom of slight depressions, and cause the, otherwise, entire margin of this 'calyx-tube' to appear lobed slightly. The main floral vascular bundle is very short, stops abruptly at the base of the flower (Fig. 3), where it is rather the meeting-point of the three carpellary vascular bundles. The central strand of tissue of the flower forms a continuous tract with the tissue of the base of the placenta. Surrounding this central strand are several layers of thin-walled empty cells, the strand itself being formed of thicker walled oblong cells (Fig. 4).

Morphology of the Female Flower.

As the orientation of the flower is unknown [1], I have made a floral diagram (Fig. 11). There was no trace of any structure which could be regarded as the apex of a lateral dwarf branch, on which the two flowers in the axil of the scale could arise. The odd seta is posterior, the three carpels, ovules, and stylar lobes are opposite one another and alternate with the setae. The male flower is naked, it may be that the female flower is also. The setae are hypogynous and arise external to the 'calyx-tube.' If the female flower is naked the setae may be staminodes (corresponding to the rudimentary ovarium in the ♂ flower). Their position (orientation $\frac{1}{2}$) is, however, different from that in all other Santalaceae [2]. If they are staminodes the 'calyx-tube'

[1] Eichler, Blüthendiagramme, p. 543.

[2] Ibid. p. 537.

cannot be part of the perianth (perigone), but must be of the nature of an epigynous disc. If the calyx-tube be part of the perianth, the setae may be an outer whorl of the same, an epicalyx, or a whorl of bracteoles, or the setae may be the only representatives of the perianth and the calyx-tube, an epigynous disc. So far as my own opinion on such an obscure point in systematic botany is worth giving I feel inclined to the view that the female flower is naked like the male one, that the three setae are three staminodes, comparable in the female flower to the remains of the gynaeceum in the male flower; that the 'calyx-tube' is simply an epigynous disc, and that the gynaeceum consists of three carpels, alternating with the staminodes. Van Tieghem[1], from an investigation of the flowers of *Thesium linophyllum* and *Osyris alba*, concludes, in so far as an anatomical examination of these two species permits it, that in the flower of the *Santalaceae* generally 'L'étamine y est une dépendance vasculaire de la face interne du sépale. Les trois carpelles sont vasculairement indépendants des sépales, quoique unis à eux par le parenchyme dans la majeure partie de leur étendue. L'axe floral ne se prolongue pas au-dessus de l'insertion des carpelles; mais chaque feuille carpellaire porte à sa base et en superposition avec elle un talon vasculaire; ce talon est, comme le carpelle lui-même, uni avec ses congénères dans la majeure partie de sa longueur, et il forme ainsi une colonne qui se dégage plus ou moins tôt du tissu de l'ovaire; mais il redevient libre à son sommet, et c'est dans ce sommet que se développe le sac embryonnaire qui lui donne la signification d'un ovule. A chaque carpelle correspond donc un ovule, et cet ovule n'est autre chose qu'un lobe pédicellé du carpelle.' Van Tieghem finds the flower of *Santalaceae* in the above features in complete agreement with that of the *Primulaceae*, as determined by himself. Eichler[2] for the *Santalaceae* and the *Loranthaceae*, and L. Jost[3] for *Viscum album* (though not

[1] Van Tieghem, Ann. Sc. Nat. sér. 5, tome xii. p. 346.
[2] Eichler, op. cit. pp. 541 and 553.
[3] L. Jost, Zur Entwick. d. Mistel, in Bot. Zeit. 1888, nos. 23 and 24.

by direct expression), are quite opposed to Van Tieghem's views. The central placenta in *Myzodendron* is, as apparently in other *Santalaceae*, axial in nature, and carries three ovules.

Nursing of the Embryo.

I shall confine my remarks, for the present, to the changes in that ovule which is destined to become the single seed of the ripe fruit. As a result of fertilisation the oosphere becomes surrounded by a cell-wall and converted into the oospore, retaining its one-sided position, to the placental side of the long axis of the ovule. The secondary nucleus of the embryo-sac divides repeatedly to give a row of nuclei extending the whole length of the embryo-sac, and soon separated from another by cell-walls, so that the interior of the embryo-sac is occupied by a uniseriate column of endosperm cells. By the time this has happened, and as a result of fertilisation, a remarkable change is observable at the narrow antipodal end of the embryo-sac, which elongates upwards and backwards in the body of the placenta, then makes a sharp bend on itself, and continues its penetrating course, in a more or less winding manner, through the free column of the placenta and on through the tract of tissue continuous with this until it reaches the base of the flower, where its tip dilates and becomes imbedded in the vascular cup, formed by the three carpellary vascular bundles diverging from the floral vascular bundle, between the tip of which and the descended tip of the embryo-sac a few layers of rich parenchymatous cells intervene (Figs. 12, 13, 14). Throughout the time of its prolongation the embryo-sac remains a uniseriate column of uninucleate richly protoplasmic cells (Figs. 12, 15), elongating apparently by apical growth, intercalary formation of new cells being very rare. The tip of the embryo-sac is pointed, ensuring a more ready passage through the placental tissue. The cross walls, which give rigidity to the penetrating sac and tend to prevent its collapse, disappear from the placental part of the embryo-sac, except at the dilated (pear-shaped)

tip, which may consist of several rows of cells (Fig. 14). The freed nuclei divide, and that part of the embryo-sac which will be called the 'placental embryo-sac tube' comes to contain a long chain of nuclei imbedded in dense granular protoplasm, for most of its extent (Fig. 18). In the meantime changes have occurred in the nucellus-part of the embryo-sac. The three or four first endosperm-cells formed here are so large as to extend, each across the whole width of the sac (Fig. 15). Their nuclei then divide several times so that each primary endosperm-cell becomes multinucleate, round each secondary nucleus a cell-wall forms, and so the nucellus part of the embryo-sac becomes filled by isodiametric endosperm-cells. The embryo, for a long time unicellular, becomes pear-shaped, and in the condition of the endosperm just described consists of several cells (Fig. 15). It remains for a long time, as in many other parasites, undifferentiated; there is no sign of a pro-embryo divisible into suspensor and terminal embryo-cell. The position of the embryo in the endosperm at this early stage is well worth noting, and one which is retained through all subsequent stages in the maturing seed (compare Figs. 15, 16). All degrees of the backward prolongation of the sac were found, from the earliest stage to its full course. Contrary, too, to what is generally supposed, all three ovules may be fertilised and the changes detailed above may occur, in part, in each one; thus there is a possibility of the presence of three young seeds in one fruit (Fig. 13). The penetration of the placenta by three elongating embryo-sacs is very rare, by two is not unusual, by one only so general that for a long time I thought, from the preparations made, it was the only case. I did not once find two prolonged embryo-sacs reaching to the base of the flower. Fig. 13 represents the usual place and stage at which the second embryo-sac ceases to develop. There can be little doubt as to the main function of the placental embryo-sac tube. The placenta is evascular, its cells are not provided with very rich contents, fusion between it and the adjacent vascular ovary wall does not take place; the distance between

the vascular bundle at the base of the flower, and the embryo-sac at its apex is relatively great, and, if the ovule is to become a seed, must be bridged over, as is done by the placental embryo-sac tube. This tube is essentially nutritive and acts as a carrier of food from the floral vascular bundle to the developing seed. By treating a longitudinal section of the placenta of a semi-mature fruit with Fehling's solution, the embryo-sac tube is found to contain abundant sugar, the presence of which and of so many nuclei in the tube tend to show that the embryo-sac prolongation has a metabolic as well as a translocating nutritive function. Only the one seed, the placental embryo-sac tube of which is fully formed, develops further. The other two, if formed at all, die at a very early stage, mainly owing to a process which is as much like strangulation as one can imagine imitated in the vegetable kingdom. The space at the disposal of the ovules in the ovary is very little, still less when the ovules become enlarging seeds, and is removed completely, contributing to the death of the other two possible seeds, by the luxuriant growth and horizontal elongation of the sterile cells of the seed destined to maturity. There is nothing in the structure of the placenta to prevent its penetration by two embryo-sacs to the base of the flower. In this case the two seeds, supposing fertilisation in the two to be simultaneous and other things to be equal, may so grow as to kill one another by mutual pressure due to the luxuriant sterile cells of the two. In the ordinary cases one seed sets up the connection with the base of the flower first, and thus gets the advantage (Fig. 14 *b*).

Returning to this seed's history it will be noticed that (Fig. 15) the true apex of the embryo-sac is still covered by the single layer of nucellus-cells. This atrophying layer is, very soon after this stage, ruptured by the growing seed to which the endosperm-cells are being steadily added at the same time that the embryo is enlarging under the influence of the feeding placental tube. In this way the seed proper comes to lie outside and below the nucellus ; the embryo-sac is not ruptured,

its wall stretches and forms the outer wall of the superficial layer of the endosperm. It is necessary to distinguish between the two directions of prolongation of the embryo-sac. The position of the unfertilised embryo-sac is represented in the seed by scarcely more than the meeting-point of the placental embryo-sac tube and the upper endosperm-cells, the seed proper lying below this meeting-point. Such is the increase in size of the seed that the thin-walled cells surrounding the central strand of cells continuous with the placental pillar are torn through; this strand with the placental column (the two containing the placental embryo-sac tube) is pushed to one side, and a single cavity extending from top to bottom of the fruit comes into existence, and is in the end as much filled by the seed as was the ovary by the ovules (Figs. 16, 17). The ripe seed is not terete but 'ovoideo-triquetrum,'[1] endosperm and embryo being, as seen in transverse sections, trigonous (Fig. 17). A comparison of Fig. 15 with Fig. 16 will show that the relative positions of the parts has remained unaltered, and will explain how the embryo is placed with radicle superior. The embryo is described in the Flora Antarctica[2], and previously by Robert Brown[3], as completely enclosed in a 'funicular membrane.' Grisebach and Hofmeister[4] were unable to find any trace of this structure, a result agreeing with the present examination. From the figures given in the Flora Antarctica it is, I think, possible to explain the cause of the contradiction of the two statements. The exact relation of the embryo to the endosperm and to the placenta has not, up to the present, been shown. It will be seen from Fig. 17 that the embryo lies in an apico-lateral lobe of the endosperm in the loop formed by the placental embryo-sac tube, and that the radicle is not exserted. The endosperm-cells enveloping

[1] Guillemin in Delessert's Icones Selectae, III, f. 47, t. 80, 1837. Guillemin, however, described the seed as pendulous from apex of locule, and saw no sign of an embryo, in *M. oblongifolium*.

[2] J. D. Hooker, op. cit. p. 301, figs. 19–21 in plate 104.

[3] R. Brown, in Trans. Linn. Soc. xix, p. 232 (note).

[4] Abhandl. Gesellsch. Götting. 1854, vols. 5 and 6. Grisebach, p. 109. Hofmeister, p. 133 (Appendix).

the upper part of the embryo are in the ripe seed empty and arranged in zones tier upon tier (Fig. 18), and look very like a distinct membrane (compare Fig. 19 with Fig. 20 in the Flora Antarctica). Longitudinal sections, however, show that these empty sheathing cells are organically continuous with the rest of the endosperm (Fig. 18). In the half-ripe seed there is a regular gradation in the diminution of contents from the lower part of the enveloping cells to the uppermost part where the endosperm-cells are empty. While this explanation seems to me to hold good for the upper part of the funicular membrane, a somewhat different one is required for the lower part, which Sir J. D. Hooker was unable to trace. In this region, owing to the pressure exerted by the enlarging embryo, the endosperm-cells adjacent to it suffer and are to a greater or less degree pressed out of shape, so that in the ripe seed the layer of endosperm-cells enveloping the cotyledonary end of the embryo may appear more or less as a thin membrane. This interpretation is supported by an examination of young seeds, in which the cells can be seen being squeezed out of shape, by comparison with the seeds of other plants, and by the frequent adherence of part of the endosperm to the embryo when the latter is removed bodily from the ripe seed which is naked, except for a small part of its surface in its apical region, where it is covered by a thin cellular membrane, apparently derived from the integument (Fig. 18, *t*).

In the ripe fruit the placental embryo-sac tube, pushed, as has been mentioned, to one side by the enlarging seed, is still an open tube, though its protoplasm is reduced to a thin layer enclosing a large quantity of cell-sap. The cell-wall of the tube is, from the first, thick and of a cellulose-nature, and in both longitudinal and transverse sections clearly recognisable as distinct from the cell-walls of adjacent penetrated cells (Figs. 18 and 19). If after dissection the placenta and seed be cleared by immersion for some time in pure glycerine, or in oil of cloves and canada balsam, and then examined, the wall and contents of the embryo-sac prolongation can be traced through the whole extent of the tube under a $\frac{1}{6}$ inch

objective, and even under an inch objective, can, in favourable examples, be traced more or less clearly (Fig. 16).

Elongation of the Embryo-sac in other Parasites.

There are many examples of an elongation of the embryo-sac at its antipodal end,[1] as well as some of an elongation at its synergidal end,[2] in the *Loranthaceae*. My impression, from an examination of the more recent publications on parasitic *Phanerogams*, was that, though it was usual, in the very closely allied order *Santalaceae*, for the apex of the sac to grow out from the ovule upwards and forwards into the ovarian cavity towards the descending pollen-tube, there was no example of a backward prolongation of the sac. It seemed to be a useful investigation to search for the existence of such a backward growth, the descriptions and illustrations of *Myzodendron* in Flora Antarctica suggesting this genus as a very suitable one for the purpose. It was not until the examination was finished that I found my impression was an erroneous one. In a report[3] by Mirbel, Brongniart, and Jussieu on a paper read by J. Decaisne in 1839, before the Academy of Science of the French Institute, the full title of the paper being 'Observations sur le développement du pollen dans le Gui, sur les changements que présentent ses ovules et ceux du Thesium,' the following paragraph occurs, 'M. Decaisne a découvert, dans ce même appareil ovulifère du Thesium, un autre organe, dont il est difficile de bien déterminer l'analogue dans tout ce que était connu jusqu'ici. C'est un tube situé longitudinalement, dans l'épaisseur de la colonne centrale, digité inférieurement, simple et renflé à son extremité supérieure qui perce la colonne et vient s'appliquer sur un point du sac embryonnaire. C'est au moment de la fécondation, où le sac embryonnaire rompt le nucelle, qu'apparaît ce tube intérieur, et qu'il perce de son côté le tissu environnant, pour se mettre en rapport avec le sac.' After a reference to Griffith's discovery of

[1] *Loranthus* and *Viscum*.

[2] Same genera.

[3] Ann. d. Sc. Nat. sér. 2, tome xiii, p. 300, Pl. 11, Figs. 12–14.

the apical outgrowth of the embryo-sac into the ovarian cavity towards the pollen-tubes in *Santalum album* [1], mention is made of the discovery by Decaisne of similar apical outgrowths in several other *Santalaceae*—in *Nanodea*, *Myoschilos*, *Osyris*, and less obscurely in *Quinchamalium*. In *Myoschilos* and in *Osyris* Decaisne again found the tube of the ovuliferous column. In *Myoschilos* a bundle of these tubes was found, five for each ovule fertilised. The nature of the tube is next discussed. The relations of its position seemed to show it was a nutritive bundle, but its structure and time of appearance were considered to support the view that it was a fertilising tube.[2]

Further, mention is made of the nearness in many respects of the *Olacineae* to the *Santalaceae*, a nearness which 'the wisdom of Rob. Brown' saw first. Decaisne thought the structure of the ovules in the two families analogous, and in one genus of the *Olacineae* (*Groutia*, Fl. Seneg. = *Opilia*, Roxb.) he found a tube placed in the ovuliferous column and passing from it to the ovule. The reporters on the paper of Decaisne saw the structures described by him. Judging from the report and especially from one of the accompanying figures (Pl. 11, Fig. 12) there is little doubt Decaisne saw, but did not recognise, a backward prolongation of the embryo-sac in *Thesium* and several other *Santalaceae* [3].

[1] Griffith, in Trans. Linn. Soc. xviii. p. 58.

[2] At this time (1840) the egg-apparatus, as such, was unknown. Schleiden's theory that the embryo was the pinched-off end of the pollen-tube penetrated into the embryo-sac, was in full force, and there were the hypothesis of 'M. Endlicher, who considers the moisture of the stigma as the fertilising substance: that of M. Schleiden, who attributes similar functions to the embryonary sac; and that of M. Unger, who believes that the pollen-grains when they arrive on the stigma are already fecundated' (Griffith).

[3] I have not been able to find any other account of Decaisne's observations on the *Santalaceae*. In the 'Nouveaux Mémoires de l'Académie de Bruxelles' (vol. xiii. 1841), a paper by Decaisne appears as 'Mémoire sur le Développement du pollen, de l'ovule et sur la structure des Liges du Gui.' In a prefatory note Decaisne states that his observations on *Loranthus* and the *Loranthaceae* generally, on the structure and development of the ovule of the *Santalaceae* and of the *Olacineae*, extending over several years and carried on independently of Griffith's, are postponed because incomplete.

In 1843 Griffith's second paper[1] was read before the Linnean Society. In this paper the embryo-sacs of *Santalum* (all three) and of *Osyris* (only one) are described as extending, 'before fertilisation,' posteriorly through nucellus and ovuliferous column to the base of the latter. Though Decaisne was the first to observe the tube in the ovuliferous column, Griffith was the first to observe its true nature. As proof of the importance Griffith attached to this backward growth of the embryo-sac I cannot do better than quote his own[2] words: 'It is probable that the curious form of embryo-sac, so conspicuous in *Santalum* and in *Osyris*, is of general occurrence in the natural family *Santalaceae*. I find, on referring to notes made in 1836, that a sac resembling that of *Osyris* at its anterior, and that of *Santalum* at its posterior end, would appear to exist in a Santalaceous genus probably allied to *Sphaerocarya*. [Foot-note] I would recommend the prolongation of a membranous tube from the base of the ovulum backwards as one test of the affinities of Santalaceae.' In 1856 Henfrey's paper 'On the development of the ovule of *Santalum album*, with some remarks on the phenomena of impregnation in Plants generally' was read[3], also, before the Linnean Society. This paper, mainly concerned in a refutation, judging from the phenomena seen in *Santalum album*, of Schleiden's theory of fertilisation and origin of the embryo (which Schleiden himself in 1858 was able to prove groundless) confirmed Griffith's description of the course of the embryo-sac, a course which may be represented as $\int_{b}^{a}$-shaped (*a* being the outgrown apical, *b* the backward grown antipodal end). In 1859 W. Hofmeister[4], extending the previous observation of *Thesium*[5], describes in considerable detail the early stages in the seed of *Thesium alpinum*, L. and *Th. intermedium*, Schrad. Decaisne's results are not noticed.

[1] Griffith, in Trans. Linn. Soc. xix (1843). [2] Ibid. p. 193.

[3] Henfrey, in Trans. Linn. Soc. xxii (1856).

[4] W. Hofmeister, Neue Beiträge z. Kenntn. d. Embr. d. Phanerog., Abhandl. d. sächs. Ges. d. Wissensch. vi, p. 563.

[5] W. Hofmeister, in Pringsheim's Jahrbücher, i. p. 112.

In *Thesium* the embryo-sac is described as stationary until after fertilisation, then, but for a short distance only, its antipodal end grows backwards in the placental pillar, as seen in Hofmeister's figures:—'Its lower portion remains during the whole further development of the seed *a simple cell* [italics mine]. Its lower end elongates to a long-drawn tube which, after perforation of the tissue of the ovule, curves vertically downwards and penetrates deep into the tissue of the ovuliferous column' (T. X. F. 3-6). Speaking of Griffith's work on the *Santalaceae*, Hofmeister says, 'The development of the seed of *Osyris* seems, from the little we know of it from Griffith, to be quite like that of *Thesium*. The embryo-sac grows out forwards from the nucellus, and extends to the base of the same.' Schacht's investigation of *Santalum album*[1] was mainly directed to a determination of the egg-apparatus and of the connection in fertilisation between the pollen-tube and the synergidae as now known, the naked apical end of the embryo-sac being very favourable for this examination. *Myzodendron* agrees with *Thesium* in the outgrowth of the synergidal end of the embryo-sac into the ovarian cavity after fertilisation, as a result of the formation of the endosperm. In this particular point *Myzodendron* and *Thesium* are distinct from *Santalum* and *Osyris*, in which the apical part of the embryo is a long, naked, projecting tube before fertilisation.

Looking at *Santalum* and *Osyris*, it would seem as if the forward upward growth of the sac was the result of a tendency of the sac to grow to meet the descending pollen-tube, much as the ovum in some animals sends out pseudopodia to meet approaching spermatozoa. This explanation of the phenomenon will scarcely apply to the case of *Myzodendron* and of *Thesium*, in which the embryo-sac before fertilisation, in so far as it is enclosed by the nucellus, is normal. It may be that in all the genera named the protrusion is due to the minuteness of the ovules, the necessity for plenty of room for the development of the seed, and for the absence of pressure in the early stages of the same.

[1] Schacht, in Pringsheim's Jahrbücher, iv, p. 1, t. 1–4.

The importance which Griffith attached to the antipodal prolongation of the embryo-sac as a character in the diagnosis of the *Santalaceae* was due to the general absence of investigations on the *Loranthaceae*. The researches of Griffith himself, of Hofmeister, Van Tieghem, Treub, and Jost have brought to light changes in the embryo-sac of different genera of *Loranthaceae*, which are in essential points similar to those occurring in the embryo-sacs of genera of *Santalaceae*, and if, as seems probable, the tube of the ovuliferous column observed by Decaisne in *Groutia*, one of the *Olacineae*, be part of the embryo-sac, a backward prolongation of the embryo-sac would rather serve as an additional point of affinity between the *Santalaceae*, *Loranthaceae*, and *Olacineae*, than as a diagnostic character of the *Santalaceae*[1]. Since the preceding was in manuscript my attention has been called by Dr. Scott to an interesting paper by L. Guignard[2] entitled 'Observations sur les Santalacées.' As *Santalum* was well known the investigation was confined mainly to *Thesium* and *Osyris*, the species being *Th. divaricatum*, Rchb., and *Osyris alba*, L. In both cases the flowers were examined from the earliest stage to the time of maturity of the fruit. In *Thesium* the archesporium of the ovule is never unicellular, usually of two cells, very rarely of more. The coming of the age of the embryo-sac is normal in both. The antipodal cells disappear very early[3] in *Thesium*, later in *Osyris*, not till fertilisation in *Santalum*. Guignard agrees with previous observers in describing the hinder part of the embryo-sac (including the placental embryo-sac tube) as uni-nucleate, the nucleus in it being the sister one of that which gives the endosperm, the two being the result of the division of the secondary embryo-sac nucleus. In *Thesium* only one embryo-sac develops, in *Osyris* all three develop and

[1] A letter from Professor I. B. Balfour cautions me against attaching too much importance, taxonomically, to the backward elongation of the embryo-sac, as such an elongation, though to a very much less extent, occurs in the root-parasites *Rhinanthus*, *Pedicularis*, etc. (Hofmeister).

[2] L. Guignard, Ann. d. Sc. Nat. sér. 7, tome ii. pp. 181, 202, Pl. 12–14, 1885.

[3] This fate of the antipodal cells helps to explain my great difficulty in seeing them in *Myzodendron*, in the material of which were no young flowers.

may be fertilised, though only one embryo forms at all. The embryos have no suspensor. The placental embryo-sac tube is present before fertilisation, elongating afterwards, but not to the same extent as in *Myzodendron*. Guignard describes a fusion of two such tubes to give a common one descending the placenta, a phenomenon reminding one of Van Tieghem's observation of *Viscum album*. Guignard agrees with Van Tieghem as regards the appendicular nature of the placenta and its ovules. This view is not supported by Guignard's own observation of *Thesium divaricatum*, in which the floral papilla, after giving off sepals, stamens, and carpels, persists as a papilla, and as it becomes covered in by the carpels elongates, simultaneously with the formation of the inferior ovary, to become the ovuliferous placenta. In this case the placenta appears to be axial in its origin. The egg-apparatus of *Santalum album* is, as described by Strasburger in his latest paper, normal. As the species observed by Guignard were, in the cases of *Thesium* and *Osyris*, hitherto unexamined, and as the results obtained were, though much more complete, not specially different from those acquired by the previous examination of other species, it would seem that there is not such a great difference between species of the same genus in the *Santalaceae* as in the *Loranthaceae* (e.g. between *Loranthus sphaerocarpus* and *L. pentandrus* as examined by Treub).

Mature Embryo.

The mature embryo of *Myzodendron punctulatum* (Fig. 20) agrees in most of its features with that of *M. brachystachyum*[1]. There is no more peculiar embryo than that of *Myzodendron* known. The viscid tissue described by Sir Joseph Hooker in *M. brachystachyum* occurs in *M. punctulatum* too, in the same position. In addition to two very small consolidated cotyledons the plumule shows a distinct projecting apex, beneath which, passing towards the radicular end, there is a well-marked procambial strand. The whole embryo is provided

[1] J. D. Hooker, op. cit. p. 301.

with a dermatogen, which here and there is divided by periclinal walls. Beneath this dermatogen, at the radicular end and extending more than a third of the length of the embryo, the viscid tissue occurs. Its cells are very long, narrow, obliquely inclined towards the axis of the embryo, and multinucleate. Running through the viscid tissue, in a position coincident with the axial plane of the embryo, there is a plate of broader and vacuolated cells dividing the viscid tissue imperfectly into two masses. A layer of empty cells extends across the embryo cutting this viscid matter off from the rest of the embryo which may be termed the germinable part. This highly differentiated mature embryo is in marked contrast with the young embryo (Fig. 21), which is undifferentiated. It may be that the viscid tissue represents the suspensor and that the closely aggregated cells in which the procambial strand ends constitute the true radicle which is then endogenous. Special pains were taken to make sure that the elongation of the embryo-sac backwards in its septate condition was not a suspensor, and strong confirmatory proof of the views previously given was furnished by one fruit in which the endosperm cells had grown round the curve of the placental embryo-sac tube and into its long arm (Fig. 22), at the same time that the embryo was distinct, independent, and in its usual position.

Germination of the Embryo, etc.

Sir Joseph Hooker has, in the Flora Antarctica, entered fully into the mode of germination of the seedling of *M. brachystachyum*, DC., as well as into the connection of the adult parasite with the host branch. As in *Viscum*, the seedling's root is independent of geotropism and its stem (hypocotyledonary) is negatively heliotropic. For interesting figures, showing the splitting into two of the viscid tissue by the growing radicle, and the mode of penetration of this to the host wood, the reader is referred to the Flora Antarctica. I was not able to observe normal germination in *M. punctu-*

latum. I luckily found three seedlings which were germinating on a branch of *M. punctulatum* itself, probably on their parent plant. Externally they were like the seedlings of *M. brachystachyum*, the radicular end was swollen and flattened, and made nearly a right angle with the curved elongated hypocotyledonary stem. The lengthened cotyledons were still enclosed in the shrivelled remains of the endosperm. Dissection of the seedling showed a well-developed axial vascular strand; stomata, as seen on the mature stem, were marked out on the hypocotyledonary stem, and there was no tendency to a separation of the outer layers of the embryo from the central parts, as seen in *M. brachystachyum*. The radicular part of the seedling was decayed and had only just begun to penetrate the branch. This decay may have been due, partly to the very thick outer epidermal wall of the branch, and partly to the fact that the seedling's host was a branch of *M. punctulatum*. In *Cuscuta*, which will not[1], as a seedling, climb round a dead support, one may see many examples of two branches twining round, and sending haustoria into one another. Solms-Laubach[2] has examined the mode of attachment of *M. punctulatum* to the host branch, *Fagus Dombeyi*. From his description it seems the intra-matrical thallus of *M. punctulatum* differs somewhat from that of *M. brachystachyum* described in the Flora Antarctica. 'The Valdivian plant *Myzodendron punctulatum*, which has already been mentioned occasionally, joins on here in the structure of its solitary terminal haustorium (Plate xxiv. Fig. 4). The relations known in *Loranthus Sternbergianus* are repeated in a smaller way. The branch of *Fagus Dombeyi* is irregularly thickened at the place of attachment of the parasite; there is no indication in this species of the wood-cups described by Hooker for *M. brachystachyum*, DC. The sucker-outgrowth spreads out in the host cortex into an irregular mass sending off short, root-like branches. From

[1] Schenk's Handbuch der Botanik, 1884, p. 372 (Mohl and Koch).

[2] Solms-Laubach, Das Haustorium d. Loranth. u. d. Thallus d. Rafflesiaceen u. Balanophoreen (t. xxiv–xxvii), in Abh. d. N. Gesell. zu Halle, xiii. 1877.

its under side suckers are produced which, piercing the phloem, are distinguished by their size and width, and to this extent remind one of those of *Viscum*. They possess an axile wood mass; a meristematic zone, which was possessed, perhaps, originally, was not observed. The whole tissue of the haustorium is distinguished, like that of *Viscum* in its young state, by its green colour, and has scattered through it innumerable star-like calcium oxalate glands.' I have been able to confirm this account by examination of a region of attachment, three-quarters of an inch in diameter. The sucker-outgrowth (the intra-matrical part of the primary haustorium) is not, as seen in cross section, like a wedge driven into the host wood, but, to use a simile elsewhere employed by Solms-Laubach, 'like a saddle on a horse's back,' with large lateral flaps. From the under (concave) surface of this sucker-outgrowth a large number of suckers are given off penetrating the host-wood like medullary rays, even to the pith. The connection of the xylem elements of the suckers with those of the host is very common.

EXPLANATION OF FIGURES IN PLATES XIII AND XIV.

Illustrating Mr. T. Johnson's paper on *Myzodendron punctulatum*, Banks et Sol.

Fig. 1. Two-year-old stem, showing one female amentum; *fr.* fruit; *fl.* flower; *s.* sterile apex of amentum; *sc.* places of origin of other amenta not figured. × 4.

Fig. 2. Transverse section of tubercle of stem; *g.* air-chamber and guard-cells of stoma. Long axis of guard-cells parallel to long axis of stem. × 480.

Fig. 3. Transverse section of two-year-old stem. *s.* sclerenchyma; *p.* pith; *ph.* phloem groups. × 50.

Fig. 4. Longitudinal median section of female flower. A look at the floral diagram (Fig. 11) will be useful. *o.* ovule; *o. c.* ovarian cavity; *pl. c.* placental column; *p.* epigynous sheath; *st.* stylar lobe; *a.* place of rupture of style in ripe fruit; *v. b. c.* carpellary vascular bundle; *pl. p.* placental tract; *t.* hairs of seta; *s. v. b.* vasc. bundle of seta; *fl.* floral vasc. bundle. × 120.

Fig. 5. Pendulous ovule in longitudinal section. *e. s.* embryo-sac; *i.* integ.; *os.* oosphere; *n.* nucellus. × 1000.

Fig. 6. Section of embryo-sac parallel to placenta and at right angles to Fig. 5. $a.^2$ antipodal cells^2; *os.* oosphere. × 480.

Fig. 7. Ovule showing *i.* integ. in surface view; *e. s.* embryo-sac; *n.* nucellus. × 1000.

Fig. 8. *a.* Seta of unfertilised flower in longitudinal section; *v. b.* vascular bundle of seta; *t.* hairs; *e.* epidermis. *b.* Transverse section of seta, same letters. *c.* xylem elements in elongated fruit-seta, showing spiral thickenings drawn out and rings separated. *d.* Surface view of epidermis of fruit-seta; *t.* base of hair. *a–d* × 480.

Fig. 9. *a.* seta of flower; *b.* seta of ripe fruit, showing hairs. × 3.

Fig. 10. Free tip of hair of fruit-seta. *m.* markings on cuticle; *w.* thickened wall beneath cuticle. × 1000.

Fig. 11. Floral diagram of female flowers. *a.* axis of amentum; *s.* seta; *c. v. b.*; *br.* bract; the three ovules are shown, the dotted lines indicate the walls of separation of the three ovarian pouches.

Fig. 12. Young seed dissected out. *endp.* endosperm; *pl. t.* placental embryo-sac tube composed of un-inucleate cells. × 480.

Fig. 13. Placenta of young fruit dissected out and flattened, showing two descending tubes *pl. t.* In *o'* the embryo-sac lost in the placenta, is apparently just beginning to elongate, cross-walls not formed. The basal part of the placental tract is not shown. × 480.

Fig. 14. Base of *pl. t.* of half-ripe seed, in carpellary vascular cup, *c. v. b.* × 1000.

Fig. 14 *b*. General view of placenta of very young fruit. *s.* seed; *d. o.* unfertilised ovules; *pl. t.* as before. × 120.

Fig. 15. Young seed in section. *n.* nucellus; rest as before. × 1000.

Fig. 16. Placenta of ripe fruit. *t.* testa; *f. p.* floor of ovary pouch; *p. c.* placental column; rest as before. × 120.

Fig. 17. Transverse section of young fruit. *v. b.* carpellary vascular bundle; *sl.* slit in which seta is lodged; *st.* stoma; rest as before. × 120.

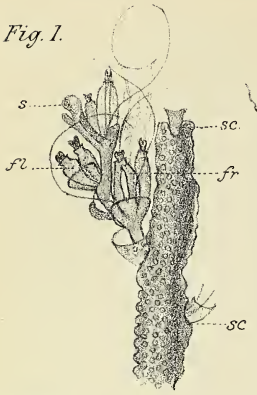
Fig. 18. A portion of nearly ripe fruit in section. *e. e.* empty endosperm cells; rest as before. × 480.

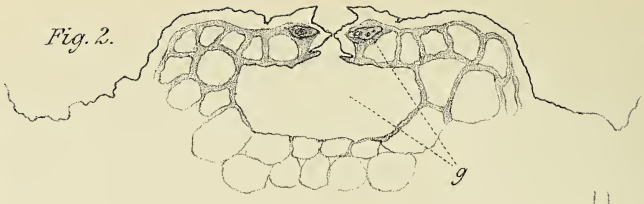
Fig. 19. Transverse section of placental tract, *pl.*, with embryo-sac prolongation in section; *c. c.* crushed cells of *pl.* In Figs. 18 and 19 the wall of the embryo-sac is seen distinct. × 1000.

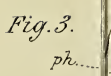
Fig. 20. Mature embryo in longitudinal section. *v. c.* viscid cells; *c.* cotyledons; *pr.* procambial strand; *r.* radicle (?); *a.* layer of empty cells. × 120.

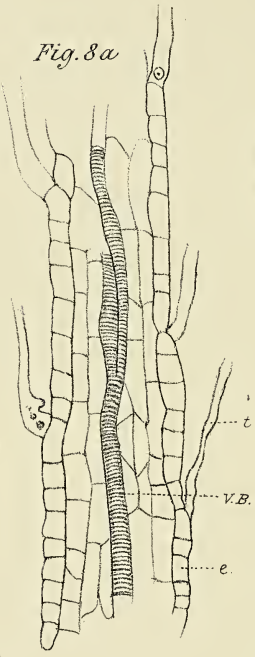
Fig. 21. Young embryo, undifferentiated. × 1000.

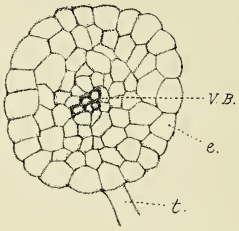
Fig. 22. Ripening seed. *endp.* endosperm cells grown round the curve of the embryo-sac (*pl. t.*) into its long arm. Other letters as before. × 480.

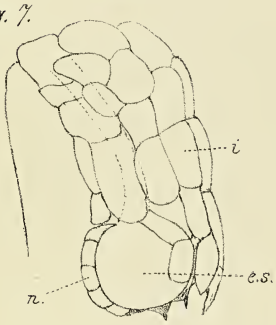


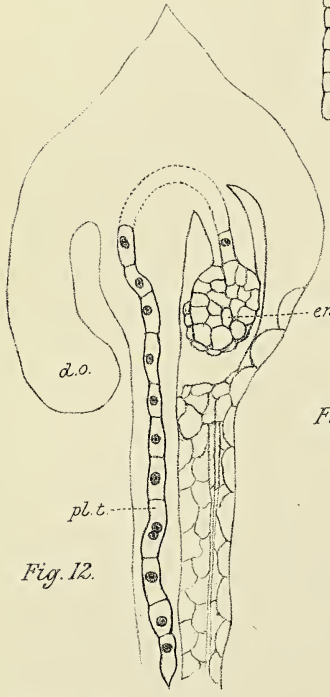


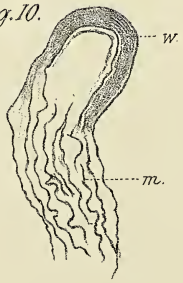


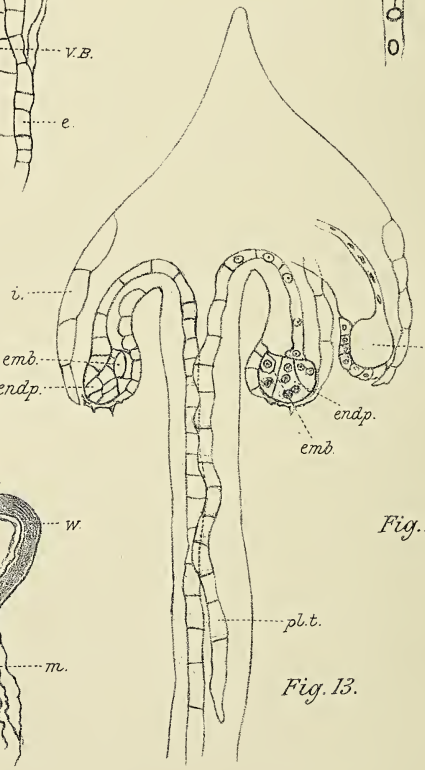












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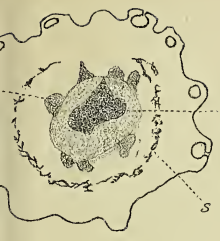

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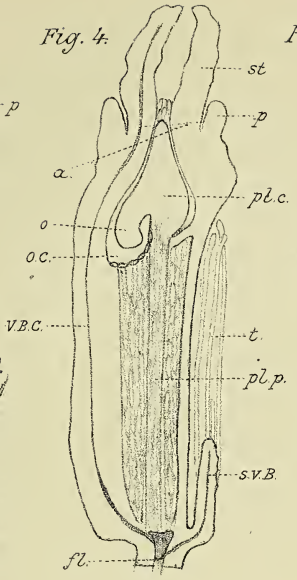

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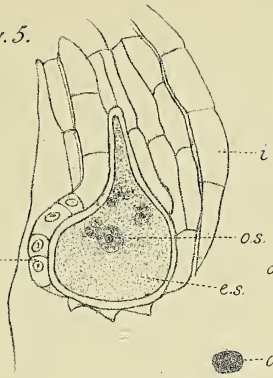

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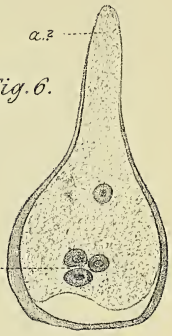

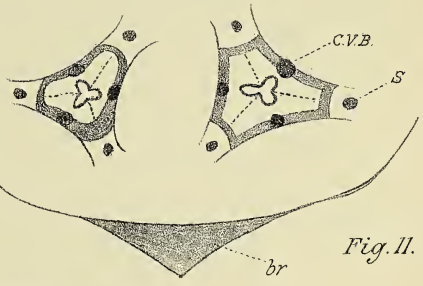

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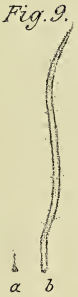

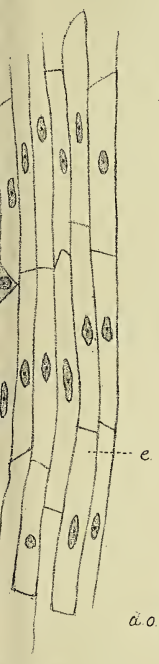

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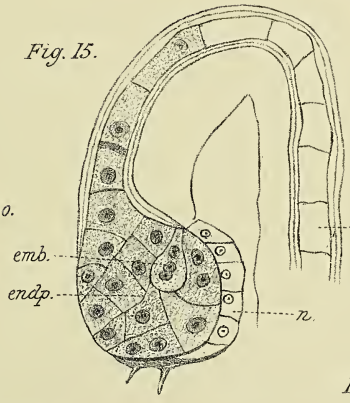


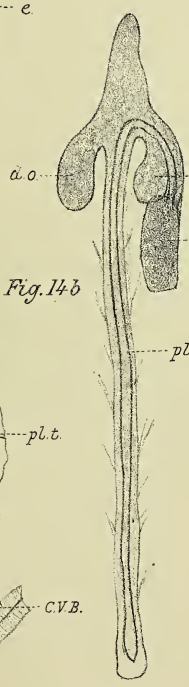
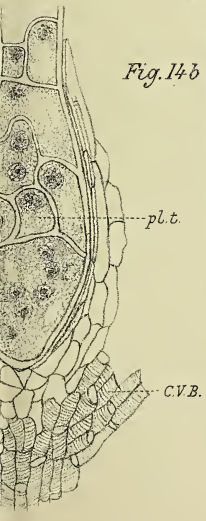


Fig. 14b



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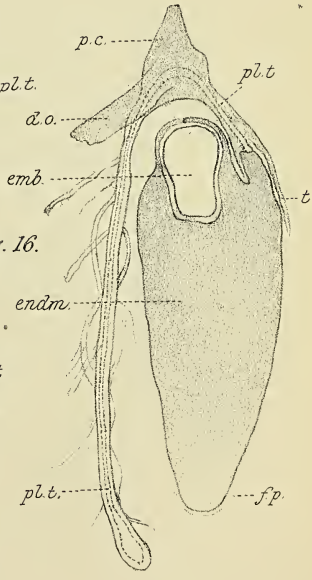

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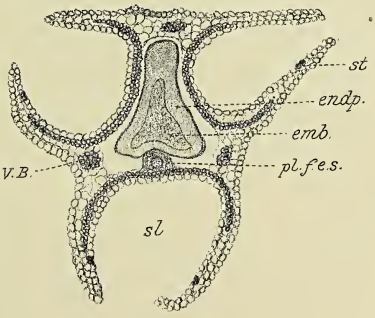

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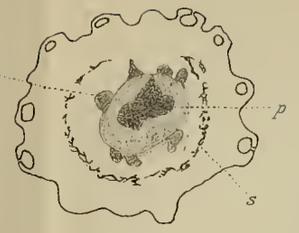
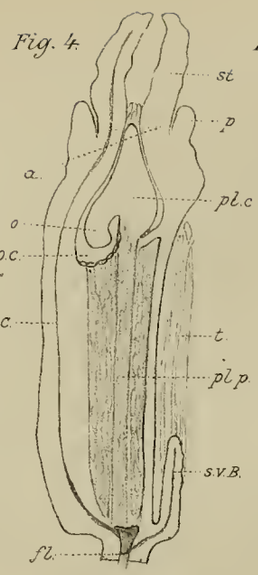
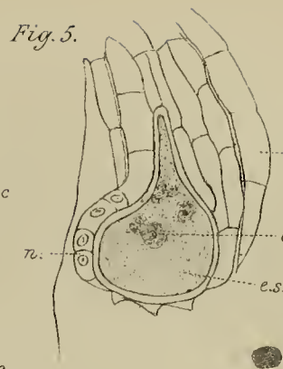
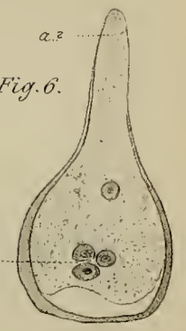
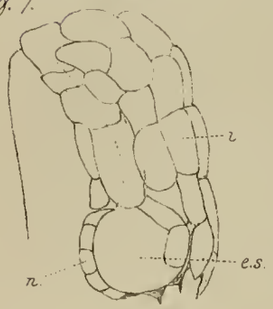
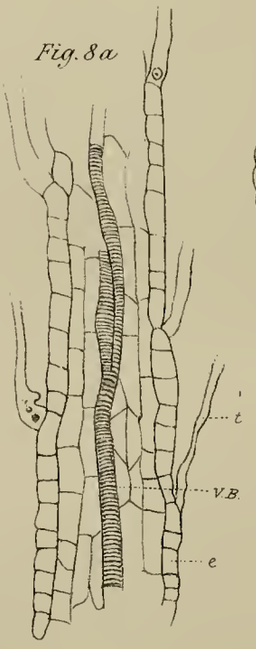


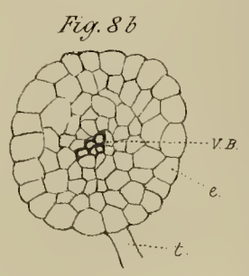


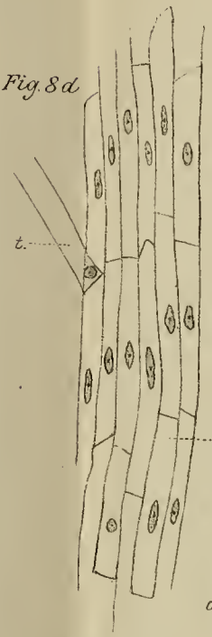












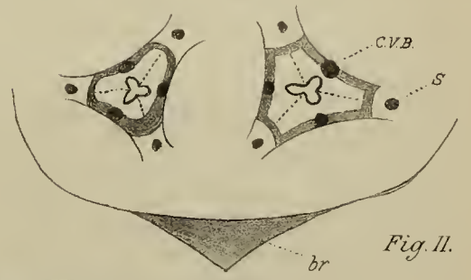


Fig. 11.

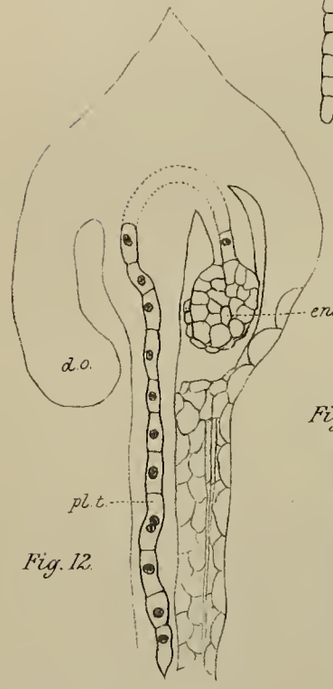


Fig. 12.

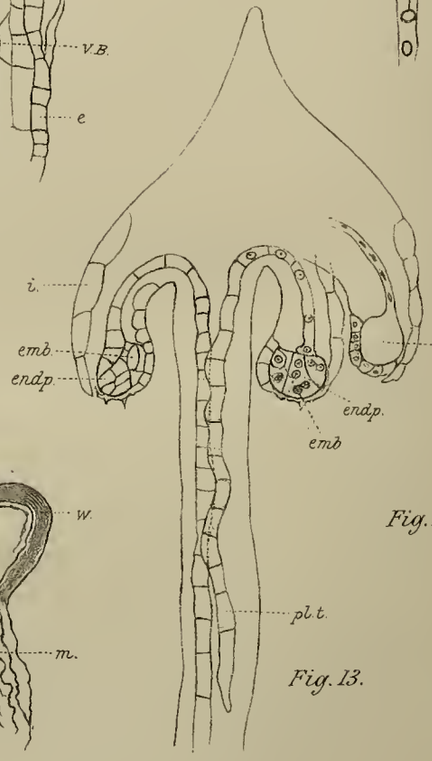


Fig. 13.

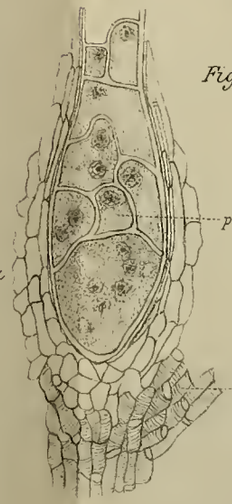


Fig. 14a.

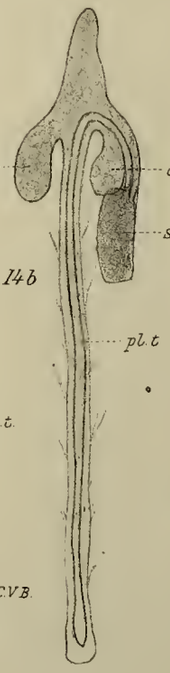
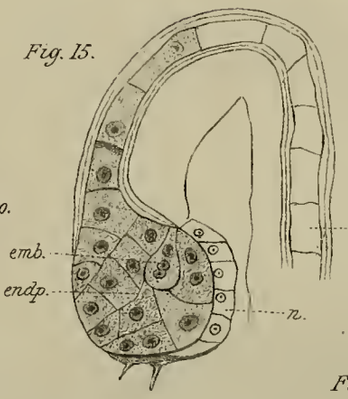
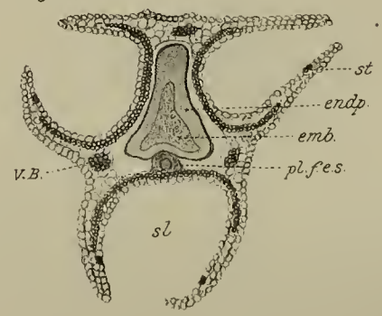


Fig. 14b.





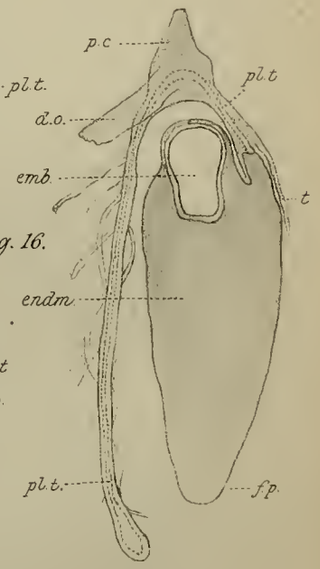


Fig. 16.

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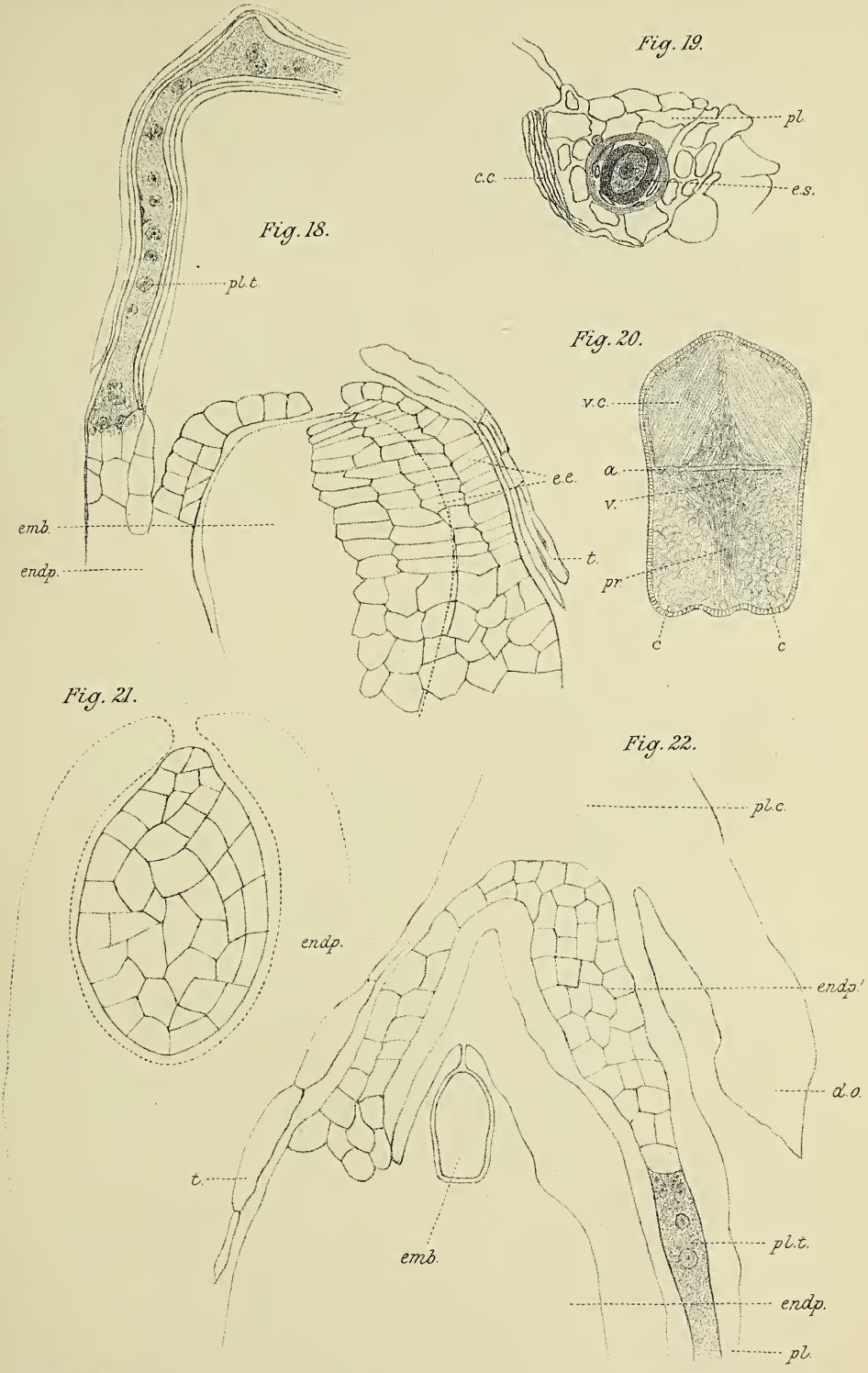

T. Johnson del

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JOHNSON.— ON MYZODENDRON PUNCTULATUM, Banks & Sol.

The Dispersion of the Spores of Fungi by the Agency of Insects, with special reference to the Phalloidei.

BY

T. WEMYSS FULTON, M.B.

With Plate XV.

1. Introductory.

IT may be desirable to explain that this investigation originated while I was engaged in the study of the adaptations of flowers for insect visits, and purely from a consideration of the possible function of the strong odour emitted by *Phallus impudicus*. It was only on the completion of my paper that I discovered that Professor Ráthay and Dr. Haas[1] had previously worked at the subject. The first notice of the probable adaptation of *Phallus* for the attraction of insects seemingly appeared anonymously in *Science Gossip*[2], and a fuller account by 'W. R. G.' in the *Bulletin of the Torrey Botanical Club* in the following year[3]. But these notices were more in the way of surmise than as showing the results of systematic investigation. The paper referred to by Messrs. Ráthay and Haas embodies the results of observation and of chemical analysis of the sporiferous hymenial slime, and indicates the adaptation of *Phallus* and its congeners for insect visitation. In the following paper the research is carried

[1] Sitzungsb. d. Mathem.-Naturwiss. Akad. d. Wissenschaft., Bd. lxxxvii, Heft 1, p. 18. Wien, 1883.

[2] November 1879.

[3] Vol. vii, p. 30, 1880.

further, inasmuch as the spores were successfully germinated, and a comparative analysis of the physical properties of the *Phalloidei* is given.

2. Phallus Impudicus.

In the case of Cryptogams the dispersal of the spores usually takes place in a purely fortuitous manner, multitudes being blown about by the wind or carried by the movement of water. But among some of the higher and most complex fungi there exist contrivances and adaptations as remarkable and advantageous as among the Phanerogams, by which the more definite and purposive actions of insects are utilised for the dissemination of the spores.

I have been able to investigate the subject completely only in the case of one fungus, *Phallus impudicus*, the common 'Stinkhorn' of our woods; but the conclusions will be found to apply to many others.

The histology and development of *Phallus* have been described by Berkeley[1], Corda[2], Lespiault[3], Rossmann[4], and especially De Bary[5], and several members of the group more recently by Fischer[6]; but to understand the adaptations for the dispersion of the spores it will be necessary to give a brief account of its structure and life-history.

Phallus is chiefly found in woods, but may also occur elsewhere—as in gardens, fields, etc.

The hymenophore or reproductive portion consists in its earliest stages of minute swellings, which arise on the underground mycelium. These at first are homogeneous, but gradual differentiation goes on, so that towards maturity the following parts may be recognised: (1) An enclosing cortical portion, the volva or peridium, composed of three layers; (*a*) an outer

[1] Ann. Nat. Hist., vol. iv, p. 158, Pl. V, 1840.
[2] Icones Fungorum, Tom. v, p. 71, Taf. VII, 1842.
[3] Ann. d. Sci. Nat., Sér. 5, Tom. iv, p. 44, Pl. I, 1845.
[4] Bot. Zeit., 1853, p. 185, Taf. IV.
[5] Vergleich. Morphol. u. Biol. der Pilze, p. 346, 1884.
[6] Ann. du Jardin botanique de Buitenzorg, vol. vi, part 1, p. 1, Pls. I–V, 1886.

firm skin or membrane, the external peridium; (*b*) an inner thin membrane, the internal peridium; (*c*) an intermediate much thicker layer of translucent, pale yellowish-brown gelatinous material, the gelatinous layer. At the base there is a cup-shaped portion which supports the stem, and is continuous laterally by its margin with the peridial layers, and below with the mycelium. (2) A central medullary portion, composed of two very different structures: (*a*) the gleba, or spore-bearing part, which forms a hollow conical cap, lying within the inner peridium and surrounding the upper portion of the stem, to the apex of which it is firmly attached. Its outer surface bears the hymenium, and is honeycombed by a large number of irregular chambers or depressions, in which the mass of spores is lodged. (*b*) The stem, consisting of a cylinder whose walls at this stage are firm and solid-looking, and composed of a multitude of small, vertically compressed cavities filled with jelly.

The volva is at first concealed beneath the surface of the soil, but towards maturity it breaks through the ground, and the exposed part gradually becomes conical and finally ruptures, the stem rapidly lengthening and elevating the gleba in the air. These phenomena depend upon a peculiar mechanical change which occurs in the stem. The gelatinous contents of the flattened cavities disappear, and they become excessively dilated, the previously compact stem increasing threefold or fourfold in magnitude and becoming open and spongy, the distension of the cavities being due to the secretion of air[1]. The protrusion and elevation of the gleba take place with great rapidity, and may be completed in from half-an-hour to two or three hours, the gleba attaining a height of from 5 or 6 to 8 or 10 inches above the surface of the ground. The utility of this sudden elevation by the substitution of a rapid mechanical process for the slower process of simple growth will be evident in the sequel.

At the time of emergence, and for a brief interval afterwards,

[1] De Bary, op. cit. p. 348. It struck me as being purely mechanical, like the expansion of a compressed sponge, air finding its way in by ruptures of the walls.

the hymenial surface is firm and solid, greenish-grey in colour, and emits a faint, mawkish, but sweetish and honey-like odour[1], which is attractive to house-flies (*Musca domestica*). Very soon, however, and before the elongation of the stem is completed, it begins to darken, the odour becomes somewhat foetid, and the consistency changes, so that it gets rather sticky and tenacious. A little later it is dark green, almost black, the odour is very strong and repulsively foetid, and its consistency slimy or almost fluid. These changes in the physical character of the hymenial mass begin at the apex of the gleba, and rapidly extend downwards. They seem to depend largely upon the influence of light, for if one side be protected from its action the change in consistency and colour is retarded on that side. A specimen I kept in a darkened place only very partially liquefied and did not drop off, but dried up into a hard, black, shining, odourless mass. When examined microscopically the foetid fluid is seen to contain myriads of spores, each 0·03 mm. long. The rupture of the peridium and the changes I have described occur during the hot months of the year, from the early part of July till the end of September, and therefore at a time when insect life is very abundant, and when myriads of flies abound. As soon as the stercoraceous odour is developed, the liquefying hymenium is visited by large numbers of flies, which sometimes, on hot sunny days, almost cover it, and suck up the fluid mass with great avidity, very soon removing the most of it. When the weather is dull and cloudy or cold fewer flies are to be seen on the glebae; but it is possible that the deliquescence then goes on more slowly.

The fact that flies are attracted to the stinking slime of *Phallus impudicus* has been long known to botanists. The earliest notice I have found of this circumstance occurs in some Latin verses[2] composed by the old botanist Hadrianus

[1] It has been shown by Messrs. Ráthay and Haas (op. cit. p. 43) that the liquefying hymenium contains three forms of sugar, laevulose, dextrose, and another, intermediate between dextrose and gum.

[2] Quoted by von Schlechtendal, Linnaea, Bd. xxxi, p. 147, 1862.

Junius, who died in 1575, but whose verses were not published until 1616. It is as follows:—

'Vertice supremo praefert exile foramen
Quod stipant avide muscarum examina nigra.'

Jacob Christian Schäffer, in 1760, described the attractiveness of *Phallus* for flies[1]. Ventenat[2], writing at the end of last century, says it diffuses 'une odeur infecte, qui attire une foule d'insectes'; and Greville[3] remarks: 'So very offensive is the smell of this substance that it is seldom allowed to drop away according to the course of nature, but is generally consumed in a few hours by flesh flies.' Berkeley[4] also says: 'The dripping hymenium affords a welcome food to multitudes of flies.'

The liquefaction of the hymenium has been generally regarded (e.g. by De Bary) as a means of allowing the spores to drop off in the fluid; but this would tend to localise rather than to scatter them. Von Schlechtendal and Dr. Cooke, however, recognised the relation of the liquefaction to insects' visits. The former says[5]:—'Dann beginnt das Hymenium und vielleicht auch die nahe gelegenen Theile zu zerfliessen, um die Sporen mit der dabei entstehenden übelriechenden Flüssigkeit zur Aussaat zu bringen, was zum Theil auch dadurch zu geschehen scheint, dass die Thierwelt, indem sie diesen sporenhaltenden Saft oder die Pilze selbst verzehrt, für deren weitere Verbreitung Sorge trägt.' Dr. Cooke[6] also surmised the value of the insects' visits when he says: 'This gelatinous substance has nevertheless a peculiar attraction for insects, and it is not altogether romantic to believe that in sucking up the fetid slime they also imbibe the spores, and transfer them from place to place, so that even amongst fungi insects aid in the dissemination of species.'

[1] Der Gichtschwamm mit grünschleimigem Hute, p. 13, 1760.
[2] Mém. de l'Instit. Nation. d. Sci. Art., Tom. i, p. 519, 1798.
[3] Scot. Crypt. Flora, vol. iv, tab. 213, 1826.
[4] Introd. Crypt. Bot., p. 347, 1857.
[5] Linnaea, Bd. xxxi, p. 115, 1862.
[6] Fungi: their Nature, Influence, and Uses, p. 123, 1875.

In regard to the insects which visit the foetid slime, I observed two species of flies ; (1) the ordinary blue-bottle (*Musca vomitoria*), which was very abundant, and (2) a large bright metallic green fly (*Musca Caesar*). On partially empty glebae which had fallen to the ground I found several small brown beetles and small dung-flies. Prof. Ráthay gives a list of fourteen species observed by him, most of which visit both dung and nectariferous flowers. It is probable that further observation will show that *Phallus* is visited by a large number of the numerous insects which visit putrid substances ; for it is evident that we have here to deal with a case of mimicry, in which such substances are successfully imitated. This is shown not merely by the physical properties of the deliquescing hymenium and the action of the flies, but also by the fact that these insects sometimes deposit their eggs on the external peridium of the burst volva, or on the ground in its immediate neighbourhood. In the majority of cases this is doubtless an instance of an instinct at fault, for I have not found a volva, *in situ*, attacked by the maggots, which probably soon perish. In one case, however, where the unruptured volva had lost its vitality while I was experimenting with it and lay loose on the surface of the soil, I found it riddled by a number of maggots which had thriven on their dietary. They were of two kinds, the ordinary maggot of the blow-fly, and one of about the same length but brown, flattened, and with lateral bristles.

Having observed the action of the flies in sucking up the spore-containing slime, the questions were naturally suggested : (1) What effect has the imbibed matter on the fly? and (2) What effect has the fly on the spores?

In order to determine these points I removed a number of nearly ripe specimens in their native earth, and placed them in town, where they could be more continuously under observation. When the characteristic odour had become developed large numbers of blow-flies rapidly made their appearance and settled on the deliquescing mass. About twenty flies were placed in a box covered with gauze, and supplied from time to time with fresh glebae.

Regarding the first question, the action on the fly, there was no deleterious effect. They lived for about three weeks on this food and then died, and as was to be expected no subsequent change occurred in their bodies.

With respect to the second question, the effect on the spores, it was found in the first place, by microscopical examination, that thousands of spores clung to the feet and proboscides of the flies. These would obviously retain their vitality. The excrements of the flies which soon covered the inside of the box, at first consisted chiefly and then exclusively of spores, microscopically indistinguishable from those directly removed from the gleba.

It was thus clear that the flies transported the spores, but the question was still to be decided whether the spores retained their vitality after passing through the digestive system of the insect, or whether, on the other hand, it was destroyed.

On *a priori* grounds this question would be answered in the affirmative. The rapid mimetic changes in the hymenium, the luring of large numbers of flies, and the fact that the flies carry off the great majority of the spores which they subsequently deposit, all point to adaptation; and to suppose that the vitality of the spores was destroyed would be to assume that a species might with impunity offer facilities for its own extinction. To experimentally determine the point, I adopted the following method for the germination of the spores. A quantity of earth taken from the place where the fungus grew was sterilised by prolonged boiling, and two series of open glass tubes were filled with this and with certain substances as shown in Table I. One tube in each series contained the same material, and to all those of *one* series was added the sporiferous deposit of the flies. Thus each experiment was duplicated, the only factor of difference being that in one series (A) the flies' excrements were present, and in the other series (B) absent. The tubes were then closed with cotton-wool and buried vertically, eight inches apart, in the locality were *Phallus impudicus* grew, near the surface but quite covered with the soil. This was done in September, and in the follow-

ing November it was found that in tubes 3 and 4 of series A a mycelium had sprouted, but not in any of the others. In December tube 3 was found lying empty on the surface, apparently thrown out by the burrowings of a mole, and its contents washed out by rain. In tube 4, however, the snowy white mycelium had increased in extent, ramification, and

TABLE I.

Contents of Tube.	Series A.		Series B.	
	With Flies' Excrements.	Result.	Without Flies' Excrements.	Result.
(*a*)	,, ,, only	No mycelium		
(*b*) Dead flies:		Do.		
1. Chopped beef	,, ,, ,,	Do.[1]	1′ ,, ,,	No mycelium[1]
2. Decaying leaves	,, ,, ,,	Do.	2′ ,, ,,	Do.
3. Rabbits' dung	,, ,, ,,	Mycelium	3′ ,, ,,	Do.
4. Faecal matter	,, ,, ,,	Do.	4′ ,, ,,	Do.

thickness[1]. Unfortunately, on re-examination in the following spring it was found to have died, and was dry, shrunk, and stained yellow. The crowning proof—the development of the hymenophore—is therefore wanting, but as the mycelium had exactly the appearance of that growing naturally and undoubtedly belonging to *Phallus impudicus*, and since it did not appear in the corresponding tubes of series B, exposed to precisely the same influences, but devoid of the sporiferous deposit of the flies, it can scarcely be doubted that it was the product of the spores contained in the latter substance, and that therefore their passage through the digestive canal of the insects does not interfere with their vitality[2].

[1] In tubes 1 and 1′ a fine mould had developed, but not apparently in 4 and 4′.

[2] The mycelium developed in the above experiment was evidently formed by a combination of hyphae from many spores. It does not appear to have been pointed out that the origination of a new individual by the union of the products of spores derived from different individuals of the same species, serves among Cryptogams the same function as cross-fertilisation does among higher organisms. In both cases the new organism is generally the joint product of more than one individual.

We thus see that insects are normally the disseminators of the spores of *Phallus impudicus*, and this fact serves to explain not only the peculiar liquefaction of the hymenium, but many other points in its structure, and furnishes, indeed, the clue to the curious and often *bizarre* forms of other phalloids, which have so often puzzled botanists to explain.

3. The Coprini.

It seems very probable that most or all of those fungi whose spores are ultimately contained in a slimy or liquid substance of dark colour, especially if of foetid odour, and which is freely accessible, will be found to have their spores largely transported by the agency of insects.

We find, for instance, in the genus *Coprinus* many examples fulfilling these conditions. There are between thirty and forty British species of *Coprini*[1], and a brief consideration of their leading characters will not be without interest. The hymenophore, which may vary in height from about half an inch to six or seven inches, is often very delicate and fugacious, and may in some cases go through all its stages and disappear within twenty-four hours or less. The stem is almost invariably white, and the external surface of the pileus is usually whitish, slate-coloured or brown, sometimes with a reddish tinge, and generally darkens in association with the change in colour of the gills, which in the majority of cases are at first white or pale or pinkish, but ultimately become almost or quite black. In some cases the pileus is conspicuous by its colouring, as in *Coprinus picaceus*, in which the outer surface is pied with white patches on a dark ground. The great character, however, of the *Coprini* is that the hymenial surface deliquesces, the spores becoming immersed in an inky-black fluid, often exceedingly foetid[2]. As is the rule in the Agaricini, the hymenium is in-

[1] Cooke, Handbook Brit. Fung. vol. i, p. 160, et seq. 1871; Illustrations Brit. Fung. Nos. xlii–xliv. Pls. 658–687, 1886.

[2] Dr. Haas found glucose in the deliquescing fluid of some species of *Coprini*. Op. cit. p. 43.

ferior and therefore not so freely exposed as in *Phallus impudicus*, but it is interesting to note that the marginal zone of the pileus generally becomes radially cleft and split up in a stellate manner, the rays thus formed usually curling up so that the hymenial surface is freely exposed, and the whole pileus may resemble an umbrella turned inside out (Pl. XV, Fig. 9). In *Coprinus fimentarius* the revolute pileus may droop, flower-like, owing to flaccidity of the portion of the stem just below it[1]. In some cases, from the radial fissuring and the curling up of the pileus, combined with peculiarities of colouring, a curious superficial resemblance to the flowers of some Compositae may be recognised, the unchanged, often brownish centre representing the disc and the radiate marginal part the rays. Such may be seen in *C. oblectus*, *C. fimetarius*, var. *pullatus*, *C. aratus*, *C. papillatus*, *C. Hendersonii*, *C. narcoticus*, *C. nycthemerus*, *C. radiatus*, and *C. spraguei*[2]. This partial mimicry may possibly be accidental and without advantage, but it is worth noting that the great majority of those species which are markedly revolute, or what I may call flower-like, grow on dung, where flies are abundant, while of those which possess neither of these characters well marked the majority do not grow on dung as a rule. We find further that in many Compositae flies form a large proportion of the floral visitors: in the ox-eye daisy (*Chrysanthemum Leucanthemum*) 36 per cent.[3]; in the daisy (*Bellis perennis*) 48 per cent.[4]; in the wild Chamomile (*Matricaria Chamomila*), which has a strong odour, 65 per cent.[5]; and in each case some of the flies habitually affect putrid substances also. Considering all these facts in relation to the *Coprini*, the assumption is certainly warranted that they exhibit adaptations for the purpose of having their spores transported by insects.

[1] Cooke, op. cit. Pl. 669.
[2] Op. cit. Pls. 661, 669, 675, 676, 680, 682, 683.
[3] Müller's Fertilisation of Flowers (Eng. Transl.), p. 331, 1883.
[4] Op. cit. p. 321.
[5] Op. cit. p. 332.

4. The Phalloidei Generally.

It is however in the Phalloidei, the group to which *Phallus* belongs, that we find the most striking and curious instances of deviation and modification for the purpose of adapting them for the attraction of insects. Their chief and central character, from the point of view of function, is the production, as in *Coprinus*, of a dark, usually foetid fluid, which contains the spores; but this leading feature is supplemented and aided by the development of a receptacle, remarkable and very various in shape, colour, and structure.

The Phalloidei are pre-eminently an order belonging to warm countries, the greater number of the species being confined to tropical or subtropical regions, where of course insect life is most abundant. Although they are widely distributed in these regions (*vide* Table II), we have only four species in Britain, and only one that is at all common, namely *Phallus impudicus*.

They are characterised by the development of the hymenium within a complete volva, usually subterranean and possessing an intermediate gelatinous layer[1]. When the spores are mature and ready for dispersion the volva is ruptured by the rapid mechanical expansion of the receptacle, and the hymenium deliquesces, darkens, and generally becomes foetid. The phenomena connected with the exposure and liquefaction of the hymenium are usually very rapid.

If we consider the character of the receptacle after its escape from the volva we find that it presents considerable variety of

[1] To this glutinous layer, which appears at an early stage, before the formation of the hymenium, various functions have been assigned. It is often regarded as serving to support the expanded receptacle by clasping it after the rupture of the peridium. But it is probable that it may have a protective or defensive function against the attacks of insects; for while many or most of the Agarici and other Hymenomycetes in the wood where *Phallus* grows are ravaged by insects or slugs, I have not found an example of the volva of the latter being attacked, although the stem after its emergence is sometimes eaten by slugs. That the interior is nutritious is shown by the case above cited, in which the maggots no doubt made their way in by the base, where the gelatinous layer is absent, and which is normally always concealed underground.

form, but that the same result of freely exposing the sporiferous slime is attained in each case.

We may divide the different species into two great types for our present purpose.

I. Stalked forms, in which the deliquescing hymenium is superior.

II. Latticed forms, in which the hymenium is contained within a sessile lattice or meshwork.

The first group may be subdivided into three subsidiary ones ; (*a*) those with a simple stalk ; (*b*) those with a velum, or reticulated expansion surrounding the stem ; (*c*) those with the upper portion of the receptacle divided into rays and more or less expanded.

There are several forms which show points of transition. The latticed forms may have a rudimentary stalk (e. g. *Colus*), or the stalked forms a sort of lattice on the pileus (some species of *Simblum*, *Foetidaria*), etc.

I have given below in Table II a list of all the species of the order of which I have been able to find descriptions or figures, tabulating the colour of the receptacle, external peridium, and sporiferous slime, the odour, the habitat, and the approximate dimensions. In many cases data are wanting ; but it must not be assumed that where no odour is stated the species necessarily had none, for many have been described from dried specimens preserved in spirits, and in some cases systematists have apparently not thought it worth while to give all the particulars.

TABLE II.

I. Stalked Forms.

A. *Without Veil or Rays.*

Species.	Colour.			Odour.	Habitat.	Approximate Height in Millimetres.
	Receptacle.	External Peridium.	Deliquescing Hymenium.			
1.[1] *Phallus impudicus*, Lin.	Snowy white[2]	White	Blackish green	Very foetid	Usually bare ground, woods, gardens, &c. Europe	230
2. *Phallus iosmos*, Berk.	Pale reddish grey	Yellowish white	?	?[3]	Sandhills, Lowestoft	120
3. *Phallus Novae-Hollandiae*, Corda	White	White	Blackish green	?	New South Wales	140
4. *Phallus curtus*, Berk.	Dirty white	Yellowish white	Olive-green	Extremely foetid	On the ground, Australia	25
5. *Phallus campanulatus*, Berk.	Dirty white	?	Greenish black	'Scarcely offensive'	On sand-dunes, Uraguay	140
6. *Phallus rubicundus*, Bosc.	Red	Grey	Brown	Foetid	Carolina	175
7. *Phallus xylogenus*, Mont.	White	Blackish	? Blackish	?	On rotten wood, Cayenne	12
8. *Phallus canariensis*, Mont.	Rose-red	Rose-red	?	?	On the ground, Canary Islands	95
9. *Phallus roseus*, Delile.	Reddish	?	Dark	?	Egypt	
10. *Phallus Watsoni*, Berk.	Pileus red	?	?	?	Australia	75
11. *Ithyphallus* (*Phallus*) *tenuis*, Fischer.	Bright creamy yellow.	?	Olive green	No odour	Fallen trunks, Java.	100
12. *Phallus* sp.	Deep red	?	?	?	Ceylon	

[1] The figures refer to the Bibliography, p. 235. [2] Red varieties have been described.

[3] Curtis, who discovered and first figured this species, says it 'had a scent somewhat like violets at a distance, when growing, but was very offensive when dried'; but, as Berkeley remarks, this is so much opposed to the general rule that it stand in needs of confirmation.

A. *Without Veil or Rays* (continued).

Species.	Colour.			Odour.	Habitat.	Approximate Height in Millimetres.
	Receptacle.	External Peridium.	Deliquescing Hymenium.			
13. *Cynophallus caninus*, Fries	White, orange or pinkish; pileus red	Brownish white	Olive-green	Foetid	Amongst decayed leaves in woods, Europe	
14. *Cynophallus bambusinus*, Zöll.	Stem rose red; pileus deep purple red	White	?	?	On bamboo trunks, Java	150
15. *Dictyophallus aurantiacus*, Mont.	Orange	White	? Dark orange red (Corda)	Foetid	Bare ground, Pondicherry	90
16. *Staurophallus Senegalensis*, Mont.	White	White	?	?	On rotten wood, Senegal	240
17. *Aserophallus cruciatus*, Lepr. et Mont.	White	White	Dark olive	?	On rotten wood, Cayenne	20
18. *Simblum peri-phragmoides*, Klotsch	Yellowish	White	Dark green	Foetid	On the ground, Mauritius	90
19. *Simblum gracile*, Berk.	Pale yellow	?	Blackish	?	On the ground in open places, Ceylon	90
20. *Simblum sphaerocephalum*, Schlecht.	Brick-red	White	Dark violet	'Horribly foetid'	On the ground in woods, South America	100
21. *Simblum flavescens*, Kurtz	Yellow	?	Olive	?	On bamboo trunks, Java	150
22. *Foetidaria Coccinea*, Aug. St. Hil.	Scarlet	White	?	Extremely foetid	Cultivated places, Brazil	140
23. '*Phallus impudicus*,' Loureiro [1]	White; cap or ? velum reddish	?	?	Foetid	By hedges, Cochin China	
24. '*Clathrus campana*,' Loureiro [1]	White	White	?	Foetid	Gardens, Cochin China	125

[1] These two species have doubtful affinities (see von Schlechtendal, Linnaea, Bd. xxxi, p. 194).

B. *With Veil.*

Species.	Colour.			Odour.	Habitat.	Approximate Dimensions in Millimetres.	
	Receptacle.	External Peridium.	Deliquescing Hymenium.			Height.	Breadth of Veil.
25. *Dictyophora indusiatus*, Ventenat	White; veil becomes reddish	?	?	Not foetid	Surinam, Cayenne	150	38
26. *Dictyophora brasiliensis*, Schlecht.	White	?	Dark olive	?	Brazil	150	75
27. *Dictyophora Daemonum*, Rumph.	White or delicate yellow	Grey	?	Foetid	India, Ceylon, Java		
28. *Dictyophora speciosa*, Klotsch	White	?	?	?	On the ground, Luzon, Philippines	140	145
29. *Dictyophora tahitiensis*, Schlecht.	White	?	?	?	Tahiti	140	75(?)
30. *Dictyophora radicatus*, Mont.	'Totus fuliginosus'	Pinkish brown	Olive-green	?	On the ground, Cayenne	100	60
31. *Dictyophora duplicatus*, Bosc.	White; pileus yellow	Greyish	?	Very foetid	Carolina		
32. *Dictyophora tunicatus*, Turp.	White	Whitish	Dark green	?	? Domingo, Guiana, Angola	150	80
33. *Dictyophora subuculatus*, Mont.	Whitish	Whitish	Olive then black	Foetid	Algiers	100	
34. *Dictyophora merulina*, Berk.	Brick red	?	?	?	Java		
35. *Dictyophora phalloidea*, Lév.	White	Brownish	?	?	On the ground in woods, Java, Cuba	150	65
36. *Dictyophora campanulata*, Nees.	White	White	Brownish greeen	?	On the ground Java.	150	?

C. *With Rays.*

Species.	Colour.			Odour.	Habitat.	Approximate Dimensions in Millimetres.	
	Receptacle.	External Peridium.	Deliquescing Hymenium.			Height.	Breadth.
37. *Lysurus Mokusin*, Cibot	Stem pink; rays intense red	White	Green	Very foetid	On rotten mulberry leaves, China	75	
38. *Lysurus aseroëformis*, Corda	Stem white; rays red above, yellowish white below	White	Dark olive-green	?	Australia	140	75
39. *Lysurus Gardneri*, Berk.	White	White	Dark brown	?	On the ground, Ceylon	150	
40. *Lysurus corallocephalus*, Welw. & Curr.	Stem white; rays scarlet	Whitish	?	Foetid	Sandy, clayey soil, Angola	125	65
41. *Aseroë actinobola*, Corda	Stem pink; lower surface of rays yellow, upper surface scarlet	White	Dark brown	?	On rotten wood, Sydney	50	100
42. *Aseroë viridis*, Berk.	metallic green; or red	Whitish	?	?	Clay banks, New Zealand	25	65
43. *Aseroë rubra*, Labill.	Stem reddish; rays pale red	White	'Green'	?	Among moss and rubbish, Australia, Tasmania	60	50
44. *Aseroë pentactina*, Endlicher	Rays pale red	White	'Green'	?	Australia	60	85
45. *Aseroë Zeylanica*, Berk.	Stem pink; rays bright scarlet	Purple	'Bright purple'	?	On the ground in woods, Ceylon	50	140
46. *Aseroë Junghuhnii*, Schlecht.	Rays red	White	Blackish	?	In woods, Java	65	250
47. *Calathiscus sepia*, Mont.	Pale rose	White	Blackish	Foetid	On the ground in woods, Hindostan	114	65

II. Latticed Forms.

Species.	Colour.			Odour.	Habitat.	Approximate Dimensions in Millimetres.	
	Receptacle.	External Peridium.	Deliquescing Hymenium.			Height.	Breadth.
48. *Laternea triscapa*, Turpin	Pale vermilion; white below	White	?	?	St. Domingo. In sandy pine woods, Cuba, Chili	50	30
49. *Laternea columnata*, Bosc.	Scarlet	?	?	Very foetid	Carolina	75	
50. *Laternea pusilla*, Berk. & Curt.	Scarlet above, white below	White	?	?	On the ground, Cuba	25	
51. *Laternea angolensis*, Welw. & Curr.	Snowy white	Dusky	Black	Not foetid	Sandy soil, Angola	125	50
52. *Colus hirudinosus*, Cav. et Séch.	White below, deep orange red above	White	Dark olive	Not foetid	Amongst moss and lichens, Toulon	30	85
53. *Clathrus cancellatus*, Linn.	Scarlet [1]	White	Olive, brown, or blackish	Very foetid	On the ground in woods, &c., Europe, India, Algiers, New Zealand	110	20
54. *Clathrus pusillus*, Berk.	Bright ruby red; paler below	White	Dark green	?	On the ground, Australia	50	30
55. *Clathrus crispus*, Turpin	Orange and scarlet	White	Purple	?	On the ground and among grass, Australia, Cayenne. On rotten wood, St. Domingo, Cuba	90	85
56. *Clathrus crispus*, var. β *obovatus*, Berk.	'Salmon-coloured' [2]	White	'Brownish-green internally'	Odourless	Sand-dunes, Uruguay	75	50
57. *Clathrus delicatus*, Berk. & Broome	'Pale'	Brown	?	?	On rotten trees, Ceylon	12	
58. *Ileodictyon cibarium*, Tulasne	White	White	Blackish	'Sub-inodorous'	Meadows & woods, New Zealand		
59. *Ileodictyon gracile*, Berk.	White	White	Olive-green	?	On the ground, Australia	55	50

[1] In exceptional cases the colour of *Clathrus cancellatus* varies through orange to yellow, or through pink to white. Some enormous specimens have been described, as large as 49 by 47 centimetres (Bull. Soc. Bot. de France, Tom. xx, p. 132, 1873).

[2] Apparently described from specimens still enclosed within the peridium.

In the first group, the simple stalked forms, the deliquescing hymenium is exposed on the upper outer surface of the more or less conical or subglobose pileus (Pl. XV, Figs. 1, 2). The total height varies from scarcely half an inch to nearly or quite a foot. The colour of the receptacle is red or reddish in 45·8 per cent., white or whitish in 37·5 per cent., and yellowish in 16·6 per cent. The colour of the external peridium is given in 16 cases: in 11 (68·7 per cent.) it is white or whitish, in two yellowish white, the other three being reddish, blackish, and brownish respectively. The colour of the hymenium is given in 15 cases, and it is dark in all except *Dictyophallus aurantiacus*. The statement that the hymenium in this species is orange-red is not made by Montagne, who first described it, but by Corda[1]. It is probably a mistake, for Corda had only a dried specimen, and very likely one with a naked pileus for examination; and as the pileus itself is deep orange-red (as in *Cynophallus caninus*, where the hymenial substance is olive-green), it is probable that when Corda moistened or scraped a portion of it to examine the spores the colouring matter was communicated to the substance removed. The odour is given in 12 cases: in 11 it is more or less foetid, and in one not foetid.

In the second group the receptacle has essentially the same form as in the first, but there is the addition of a remarkable reticulated expansion attached below the pileus, usually campanulate in form and spreading out around the stem like a frill or crinoline. It may be relatively small or close to the stem, as in *Dictyophora tahitiensis*, Schlecht. (*Phallus Daemonum* of Hooker) and *Dictyophora indusiatus* (Vent.); or it may form a large network reaching nearly to the ground, as in *Dictyophora speciosa*, Klotsch, where it has a circumference of about 20 inches (Pl. XV, Fig. 4). Of the 12 species given in Table II, the receptacle in ten is white, in one brick red, and in one apparently dark. The colour of the external peridium is given in only seven cases; in five it is whitish, and in two brownish. Where described the hymenium is dark. In only four species is the odour given; in three it is foetid, and in one it is not foetid.

[1] Icon. Fung., Tom. vi, p. 19.

The third group comprises some forms very remarkable in shape and colouration. The superior margin of the receptacle is divided into erect or spreading rays. In *Lysurus Gardneri* there are five rays united at their apices, leaving vertical slits between; in *Lysurus Mokusin* there are also five, primarily apically connected, and then separate, but more or less erect. In *Lysurus aseroëformis* the rays are more numerous, irregularly dichotomous, and in the early stages in vertical apposition; but they subsequently open up and spread out like the petals of a flower (Pl. XV, Figs. 5, 5 *a*, 5 *b*). In *Calathiscus sepia* the margin of the receptacle is expanded and elevated above the hymenium in the form of a cup, with twenty narrow erect cirrhose rays. It is in the genus *Aseroë*, however, that the most striking forms are to be found (Pl. XV, Fig. 6). The rays are generally horizontal, spreading like the tentacles of an anemone, vary from five to twenty in number, and are more or less bifid. The breadth of the stellate disc varies from about 2½ inches in *Aseroë rubra*, Labill., to nearly a foot in *Aseroë Junghuhnii*. The hymenium either forms a ring around the central opening in the disc, or extends some distance on the upper surface of the rays. In eight cases the odour is not given, in the remaining three it is foetid.

In the fourth group are those species in which the receptacle is developed in the form of an ovoid or subglobose lattice, bearing the hymenium in its interior. It may be exceedingly open, as in *Laternea*, in which two (*Laternea pusilla*), three (*Laternea triscapa*), or four (*Laternea columnata*, *Laternea angolensis*) columns are apically united and widely separated; or it may be much closer, passing through such forms as *Colus hirudinosus* (Pl. XV, Fig, 7), in which the lateral columns are increased in number, and at their apices united by a localised and limited mesh-work, to *Clathrus* and *Ileodictyon*, which are subglobular and reticulate (Pl. XV, Fig. 8). Of the 12 species given in the table the receptacle in eight is red (66·6 per cent.), and in four white. The colour of the external peridium is given in 11 cases—in nine it is white, in one brown, and in one darkish. The odour is stated in six cases—in four it is not foetid, and in two foetid.

The general results in regard to colour and odour are summarised in Table III.

TABLE III.

	Colour													Odour of Deliquescing Hymenium.			
	Of Receptacle, or part conspicuous during Deliquescence of Hymenium.					Of External Peridium, which has no relation to the Deliquescence of the Hymenium,							Of Deliquescing Hymenium.				
	White or Whitish.	Red or Reddish.	Yellowish.	Green.	Dark.	White or Whitish.	Reddish.	Brownish.	Purplish.	Yellowish.	Blackish.	Not stated.	Dark.	Orange Red.	Not stated.	Foetid.	Not Foetid.	Not stated.
I. Stalked Forms. A. Without veil or rays	9	11	4			11	1	1		2	1	8	14	1(?)	9	11	1	12
I. Stalked Forms. B. With a veil	10	1			1(?)	5		2				5	5		7	3	1	7
I. Stalked Forms. C. With rays	1	10[1]		1		10			1				9		2	3		8
I. Latticed Forms.	4	8				9		2				1	8		4	2	4	6
Totals	24	30	4	1	1	35	1	5	1	2	1	14	36	1(?)	22	19	6	33

[1] *Aseroë viridis* sometimes occurs entirely red, and is included here also.

We see from this table that in the Phalloidei the receptacle, or the part that is conspicuous during the exposure of the deliquescing hymenium, is some tint of red in more than half the species, and white in nearly the other half; these two colours occurring in above 91 per cent. of the species. Those with yellow receptacles are confined, with the exception of *Ithyphallus* (*Phallus*) *tenuis*, to the genus *Simblum*, although others may have yellow tints in particular parts, or as varieties (see Table II).

The question now arises whether the colours exhibited by the receptacles of the Phalloidei correspond with the colours of the receptacle in other fungi. I give in Table IV the percentages of the colour of the receptacle in 1288 species of fungi other than Phalloidei as shown in Tulasne's Fungi Hypogaei, in Cooke's[1] plates of the Agarici in his Illustrations of British Fungi, and in Bulliard's Champignons de la France in the Herbier de la France, which comprises fungi of many groups.

TABLE IV.

	Bright Red.	Pure White.	Reddish.	Whitish.	Pure Yellow.	Yellowish.	Green or Bluish.	Purplish.	Browns, Slate, Black, &c.
	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
1. Fungi Hypogaei (44 species)	0·0	4·5	2·2	9·1	0·0	4·4	2·2	2·2	75
2. British Agarici (709 species)	1·5	6·6	3·6	8·6	1·4	3·2	0·7	?	74
3. Champignons de la France (535 species)	5·2	4·6	4·4	5·9	1·4	3·1	3·1	0·9	70·8
Average .	3·0	5·7	3·9	7·5	1·4	3·2	1·7	?	73·1

It is very clear from this table that the coloration of the Phalloidei is exceptional. We see that among them 91·5 per cent. are either red or white, while only 20·1 per cent. of

[1] Nos. 19, 20, 21, 25, 29, 30 were not accessible to me.

other fungi are so coloured; and, further, that while the great majority (73·1 per cent.) of other fungi are of dull tints —browns, slate, blacks, etc.—such colours are not represented among the Phalloidei, with the doubtful exception of *Dictyophora radicata*. And this is not all, for while a large number of those included among other fungi as red or white have impure tints, the great majority of the Phalloidei have colours very brilliant and pure.

I think the inference is evident that the brilliant tints of the Phalloidei have been developed to render them conspicuous.

The utility of a colour in making an object striking or in concealing it of course depends upon the background, and in order to test how the colours of fungi may serve for either of these purposes I made the following experiments. I placed a series of equal-sized, differently coloured discs perpendicularly in the ground in the locality where *Phallus* grows (dark-brown soil with a sprinkling of green herbs, in a wood), and observed the relative effect at various distances, with the following results: (1) Brown, blackish, and purple soon became indistinct and indistinguishable: they served to conceal. (2) Blue was fairly conspicuous near, but not at a distance. (3) Green was conspicuous against the bare soil only. (4) Pale yellow was much more conspicuous than any of the above, and to considerable distances. (5) Red was strikingly conspicuous near, and to considerable distances. (6) White was very conspicuous near, and to the greatest distance of all. A glance at the habitats of the Phalloidei, given in Table II, will show that against such backgrounds red and white and yellow must be very conspicuous. There are two apparent exceptions in the case of *Dictyophora radicatus*. Mont., and *Aseroë viridis*, Berk. The former is described as being all sooty black, and it grows on 'the ground' in Cayenne. If this be the colour of the receptacle while the hymenium is exposed, it forms a striking exception to all other Phalloidei. The case of *Aseroë viridis* is different and very interesting, inasmuch as two varieties are found, one metallic green, growing on 'clay-banks,' and the other of a more or less deep red, growing on the ground, and

presumably among green vegetation. If the clay-banks are almost destitute of green vegetation, and especially if they are whitish or reddish, the green colour of the fungus may serve to make it conspicuous. It is not stated whether it has odour or not.

As is well known from the labours of Sprengel, Darwin, Müller, and others, the colours of flowers have been gradually developed by the beneficial visits of insects, and in Table V the percentage proportions of several colours are given in the case of flowers, Phalloidei, and other fungi.

TABLE V.

	White.	Yellow.	Red.	Blue.	Violet.	Green.	Brown or blackish.
Flowers[1] (4197 species) . . .	28·5	22·6	21·96	14·1	7·3	3·6	0·5
Phalloidei { Receptacle (59 species)	40	6·4	50	0·0	0·0	1·6	1·6 (?)
Phalloidei { Volva (45 species) .	77·2	4·5	2·2	0·0	2·2	0·0	13·5
Other fungi (1288 species) . .	13·2[2]	4·6	6·9[2]		?	1·7[3]	73·1

These figures bring out very strikingly the preponderance of flower-like hues among the Phalloidei in comparison with other fungi; 73 per cent. of flowers, 96·6 per cent. of Phalloidei and only 24·7 per cent. of other fungi being either white, red, or yellow. Blue and violet, which are common enough in flowers, are rare among fungi. The reason of this comparative commonness in the former may be explained by the fact that they are, as a rule, found in highly developed flowers, which are fertilised by the more specialised insects; in other words, that these colours are the result of the effort of the flower not merely to make itself conspicuous, but at the same time to differentiate itself from the commoner colours of the more abundant flowers, so that the insect may discover the par-

[1] Köhler and Schubler, quoted in Balfour's Manual of Botany, p. 329.
[2] Including impure tints. [3] Including bluish.

ticular flower at a glance. This element of complexity in the colour-relations of flowers is absent in the case of the Phalloidei.

It will be observed that the colours of the volva do not correspond with those of the receptacle, but tend rather to approximate to those of ordinary fungi. The preponderance of white may be accounted for by this being the colour of the mycelium, and since the volva is usually subterranean, and therefore not visible during its development, there is no particular call for specialisation; but in some cases it may ultimately serve as an aid in revealing the receptacle, or as a protection by resembling the colour of its surroundings, e.g. *Phallus xylogenus,* Mont., which grows on decaying wood, and has a black peridium. There is another point in these colour-relations worthy of remark. Among flowers the part most exposed is most brightly coloured, and the colour, as a rule, is not fully developed until it is needed, i.e. when the stigma or anthers are mature and the flower is ready to open. The same is precisely the case in the Phalloidei. In *Dictyophora indusiata* (Vent.) the veil which is at first white becomes reddish as the deliquescence proceeds ('en vieillissant'), and this change or deepening of tint also occurs in *Lysurus Mokusin* (Cibot), *Lysurus aseroëformis,* Corda, *Clathrus cancellatus*, etc. Further, the most exposed part is invariably, as in flowers, the part most brilliantly coloured, as may be seen from the description of the stellate and latticed forms in Table II (pp. 222, 223), in which the upper surface of the rays and the outer and upper parts of the lattice are most brightly tinted[1]. It is also to be noted that

[1] The whole question of the function of colour in fungi in relation to their environment is one which has not yet received the attention it deserves. Grant Allen (The Colour-sense, p. 49) suggests their similarity to the 'possibly adventitious colouring of the lower animal forms, such as sea-anemones, star-fish, and medusae.' So far as my studies have gone, colour in fungi serves functionally to act on the colour-sense of animals:—(1) For concealment; hence the predominance of dull tints (Table IV), the upper part of the pileus and the lower and larger portion of the stem being usually similarly coloured and darker, the lower surfac of the pileus and the adjacent part of the stem being as a rule paler, i.e. preserving to a greater extent the primary appearance of the mycelium; (2) For con-

the foetid odour is not developed until the change in the consistency of the hymenium allows the spores to be sucked up by the flies.

In regard to odour, in the 25 species in which its presence or absence is mentioned there are 19 (76 per cent.) foetid, and six (25 per cent.) not foetid; while among the flowers of 4,189 species of phanerogams examined by Köhler and Schubler[1] only 417 (9·9 per cent.) had odour. There seems to be no relation between the presence or absence of odour and the degree of conspicuousness; the most inconspicuous (e.g. *Phallus curtus*, Berk.) and the most conspicuous forms (e.g. *Clathrus cancellatus*) may be equally foetid, and *vice versa*. The odour is sometimes most intense. Cooke[2], for instance, says:—'The experience of more than one artist, who has attempted the delineation of *Clathrus* from the life, is to the effect that the odour is unbearable even by an enthusiastic artist determined on making a sketch.'

I have mentioned the flower-like character of colour and the presence of odour, but in many cases there is a third attraction or subsidiary aid to conspicuousness in the peculiar form of the receptacle, which probably exhibits more variety in this than in any other group of fungi. In *Dictyophora*

spicuousness, and this for two purposes: (*a*) to attract insects, as in the Phalloidei: (*b*) to ward off the attacks of animals by advertising the presence of disagreeable or noxious qualities, as in the case of many poisonous fungi, and, as Darwin, Belt, and Wallace have shown, is the case among certain animals, as bitter brightly coloured caterpillars, etc.

In tabulating the colours of different groups I have been struck by the predominance of brilliant colours, especially red and yellow, among the *Pezizae*, which, differing from most of the Agarici, have the hymenial surface freely exposed, as in the Phalloidei, the spores often lying as a layer on the surface, and also among a small group of Agarici, the Amanita, many of which have beautiful tints and agreeable odours, and grow chiefly in places where insects are abundant. In such cases, and also among the Mycena and several small Agarici, it is usually the margins of the gills or lamellae which are most brightly tinted. The presence of hair-like appendages on the stem, etc., is significant from the function of such structures in relation to the floral parts of many Phanerogams, and it is worth while noting that many brightly coloured *Pezizae* have similar structures arranged like 'guards.' This aspect of fungi is well worthy of further study.

[1] Op. cit., p. 330.

[2] Fungi: their Nature, &c., p. 116.

the remarkable reticulated veil around the stem, produced by the excessive development of a small and unimportant membranous layer that exists in *Phallus*, serves materially to reveal its presence. In *Aseroë* and some species of *Lysurus* we have the assumption of the flower-like stellate form (foreshadowed in *Aserophallus* and *Staurophallus*), and it is in this group also that the most brilliant colours occur, the majority (83·3 per cent.) being vivid scarlet or red. Few flowers can compete in conspicuousness with *Aseroë Junghuhnii*, Schlecht., which forms a red star with 16 or 18 rays, and nearly a foot in diameter. The stellate form, which is assumed by so many flowers both much and little specialised, is the form (as I have shown by experiment, and planimeter measurements) which gives the maximum conspicuousness at moderate distances with the least expenditure of material. It is obvious that the lattice form also furnishes an effective and economically conspicuous receptacle.

The facts above given in reference to the form, colour, and odour of the receptacle and hymenium in the Phalloidei point to adaptation for the purpose of attracting insects, and there is direct testimony that insects do visit several of the species besides *Phallus impudicus*.

Cibot, describing *Lysurus Mokusin*, makes the following observations [1] which imply the visits of insects to the hymenial slime. 'Incrementum intra duodecim fere horarum spatium absoluit, perfectusque statim flaccescere incipit, curuatur, in se recumbit et putridinem sentit; attamen hoc illi rarius accidit, quandoquidem Insecta varia eiusdem substantiae auidissima vix terra emergentem fungum plerumque obsident et ante perfectum vegetationis stadium fere totum absumunt.' Curtis, in referring to *Phallus iosmus*, says [2], 'Flies of all descriptions were much attached to this fungus, and, as well as bees (!?) and beetles, seemed very fond of the shining matter which dropped from the pileus'; and the particular fly he describes as living upon it, and which he figures under the name of

[1] Op. cit., p. 373. [2] Loc. cit.

Borborus hamatus, is 'found on windows in houses, in marshy places, and on putrid substances, as dung-heaps, etc.' In regard to *Foetidaria coccinea*, Aug. de Saint-Hilaire, who found it, says [1], 'Cette plante a une odeur extrêmement fétide et est sans cesse couverte des mêmes mouches que l'on a coutume de voir dans le pays sur les cadavres et les végétaux en putréfaction.' Burmeister found the pileus of *Simblum sphaerocephalum*, Schlecht., covered with a dark violet, semi-fluid mass, 'an der die Fliegen eifrig saugen.' With the very doubtful exception of *Phallus iosmus*, all the above named species are foetid [2].

There is also indirect evidence of the action of flies in the fact that *Clathrus cancellatus* has been found in a wood growing close to the dead body of a dog in advanced decomposition [3], and the Italian botanist Pollini found a specimen of the same species growing on a human skull in a tomb [4]. Corda also states [5] that *Phallus impudicus* is common in Zoological Gardens and pheasanteries, where excrements are of course abundant.

In the Phalloidei then it can scarcely be doubted that we have a group of fungi which have undergone great modifications so as to become adapted for the dispersion of their spores by the agency of insects and especially by those which habitually affect putrid substances, and would therefore deposit the spores on the most suitable nidus for their growth. It is an example of the substitution of the more certain action of

[1] Op. cit., tom. iii., p. 192.

[2] I am informed by Professor Bayley Balfour and Dr. J. M. Macfarlane that specimens of *Cynophallus caninus*, which they found in a wood in Ayrshire last summer, were exceedingly attractive to flies, which were 'very like the ordinary house-fly in size and appearance.' In these specimens the stalk was yellow, and the head bright red. *Cynophallus caninus* has been hitherto described as 'scentless,' but Professor Balfour points out that the odour in the above case 'was quite conspicuous, not so strong as that of *Phallus impudicus*, but of the same character.' It is highly probable that further observations on fresh specimens of other species will reduce the number of 'odourless' forms.

[3] Bull. de la Soc. Bot. de France, tom. xx. p. 131. 1873.

[4] Loc. cit. p. 132.

[5] Icon. Fungi, loc. cit.

insects for the uncertain action of the wind, just as in the case of the cross-fertilisation of flowers, where the former agency has so largely replaced the latter. It is easy to understand the utility of this substitution, for if one consider a certain area, as a field or wood, and the proportionately small surface occupied by putrescent matter, it is evident that of the spores blown about at random by the wind the number deposited on such substances will be very small compared with the number lost. If the relative areas be as one to a thousand, on an average 999 spores will be sacrificed for every one deposited; for the agency is, so to speak, rigidly neutral and impartial. In the case of the insects, however, the proportional loss would be very much less, for, guided by their senses, they would tend to pass directly from one seat of putrid matter to another.

Now, since the sole reason of an aërial receptacle in fungi is for the formation and dispersion of the spores, it follows that the Phalloidei must be regarded as exceptionally highly organised; and I will sum up their chief characters that point to this as follows:—

(1) The formation and maturation of the spores within a closed volva, usually subterranean and protected largely from injury.

(2) The sudden emergence and expansion of the receptacle, not by the comparatively slow process of cellular growth, but by a mechanical springlike apparatus acting quickly.

(3) The freely exposed hymenium undergoing rapid mimetic changes, whereby putrid matters are simulated in colour, consistency, and usually odour.

(4) The development of a striking form, and of such colours as will make the receptacle most conspicuous, and the production of accessory parts for the same purpose.

(5) The rapidity of the whole cycle of phenomena by which the risk of accidental destruction, by animals, etc., is lessened, and the effective dispersion of the spores secured.

I may finally add a word as to the importance of these observations that flies and other insects transport living spores of

fungi in relation to the transport of bacteria. The teleology of the bad odours of putrefaction has, so far as I am aware, never been explained; but since these odours depend upon the presence of organisms, and serve to attract multitudes of flies, and since it is a rule in Nature that no organism aids another except, so to speak, with the object of ultimately benefitting itself, it seems to me highly probable that the odour of putrescent matter has been developed in relation to the visits of flies. The advantage to the bacteria is obvious, for by the odour produced, the irregular fortuitous action of the wind is largely replaced by the direct purposive action of insects; and hence, once the odour is developed, flies will form the chief means of dispersal. It has been shown above that spores may retain their vitality during their passage through the digestive canal of flies, and there can be little doubt the same applies to bacteria. Flies may thus serve to disperse not only the micro-organisms associated with putrefaction, but also those which are the cause of certain diseases, such as anthrax, etc., in which the products are attractive to them; and since flies, apart from their own powers of locomotion, are known to be carried long journeys in railway trains and steamers, they may serve to carry infection and spread diseases to distant places.

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3. Corda, Icon. Fung., tom. vi, p. 19, Taf. III, Fig. 46.

4. Hooker's Journ. Bot., vol. iv, p. 69, 1845; Corda, Icon. Fung., tom. vi, p. 19, Taf. III, Fig. 47.

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EXPLANATION OF FIGURES IN PLATE XV.

Illustrating Dr. T. Wemyss Fulton's paper on Dispersion of Spores of Fungi by the Agency of Insects.

Fig. 1. *Phallus curtus*, Berk. (after Corda).

Fig. 2. *Aserophallus cruciatus*, Lepr. et Mont.

Fig. 3. *Simblum periphragmoides*, Klotsch.

Fig. 4. *Dictyophora speciosa*, Klotsch (reduced $\frac{1}{2}$).

Fig. 5. *Lysurus aseroëformis*, Corda. 5 *a*, 5 *b* showing the progressive expansion of the rays.

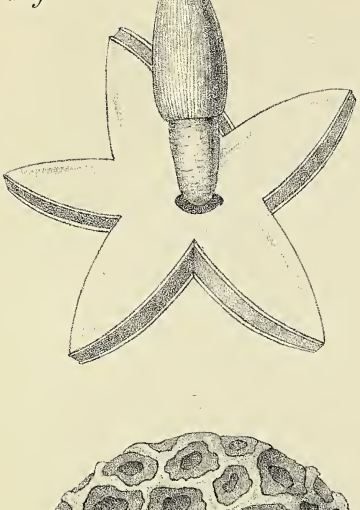
Fig. 6. *Aseroë actinobola*, Corda (after Berkeley).

Fig. 7. *Colus hirudinosus*, Cav. et Séch.

Fig. 8. *Clathrus pusillus*, Berkeley.

Fig. 9. *Coprinus deliquescens* (after Bulliard).

Fig. 1.



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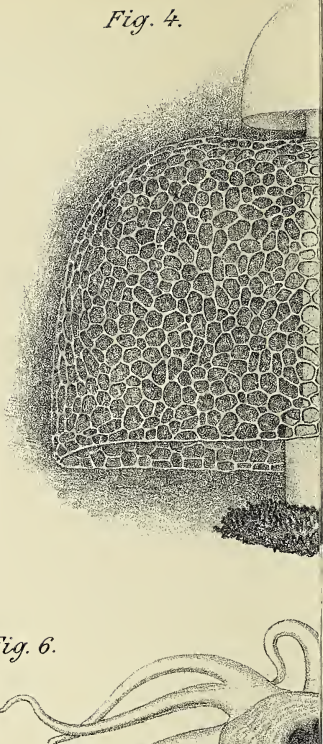

Fig. 3.

Fig. 6.

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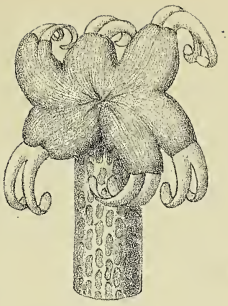
Fig. 5 a



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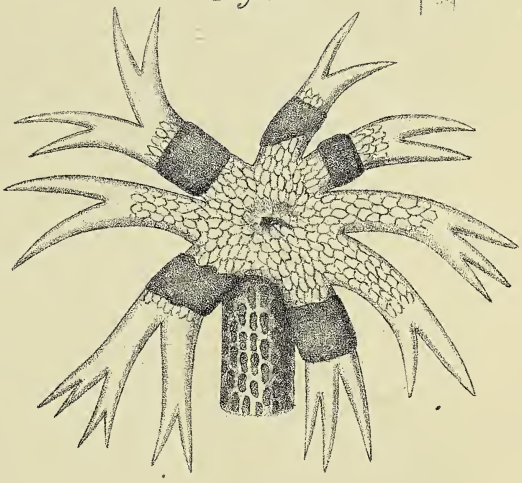

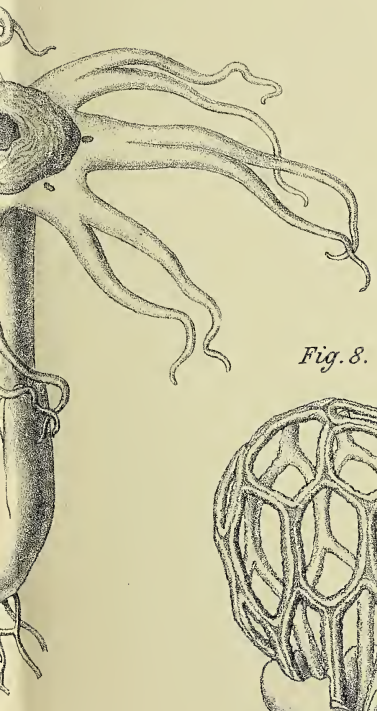

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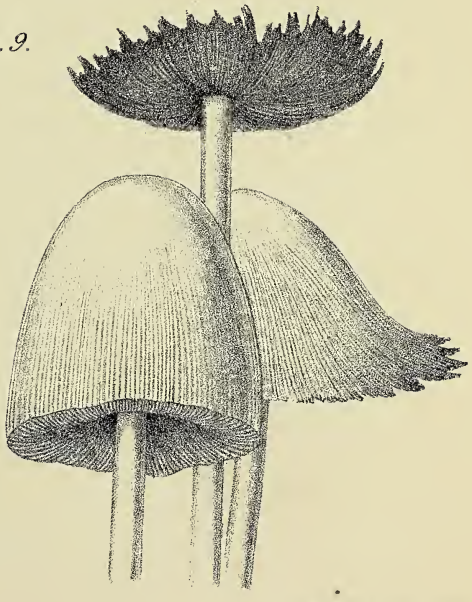

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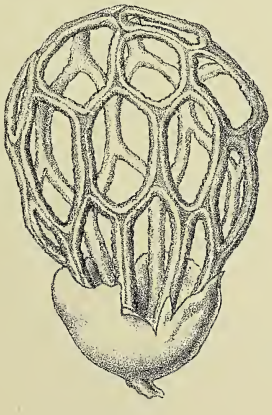
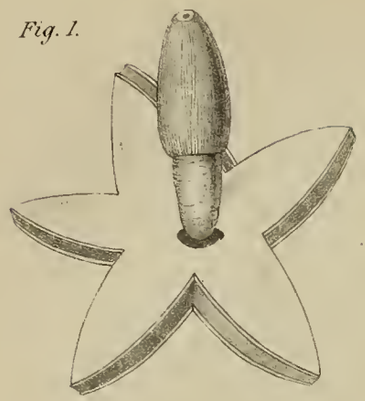


University Press, Oxford.

Fig. 1.



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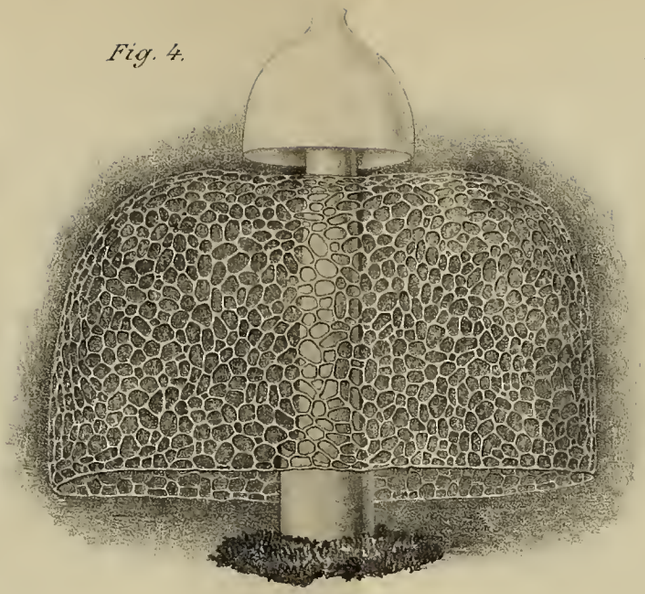
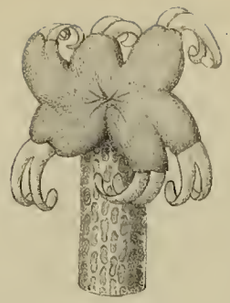


Fig. 5 a.



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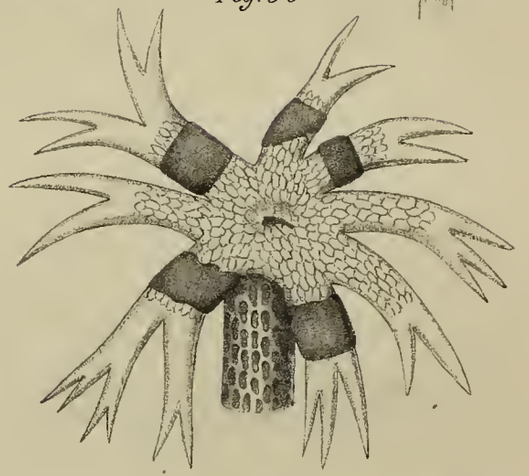

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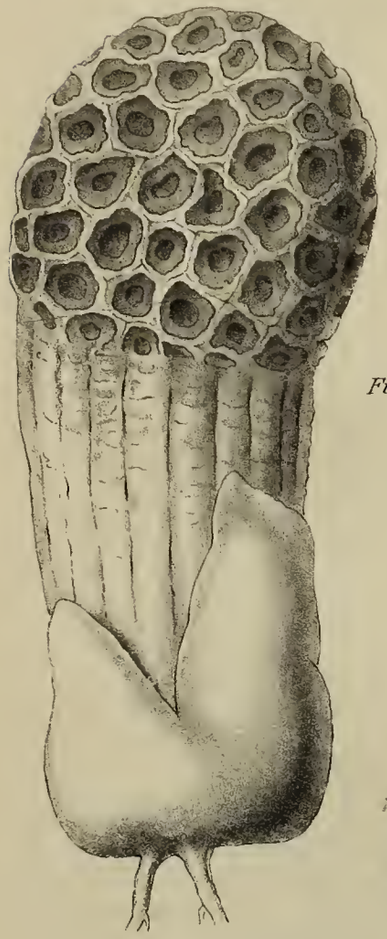

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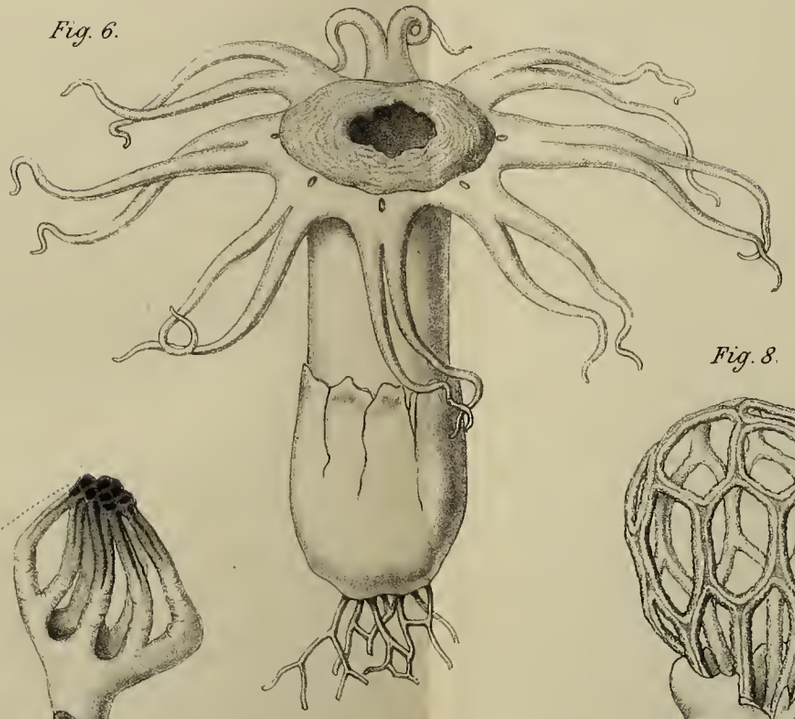

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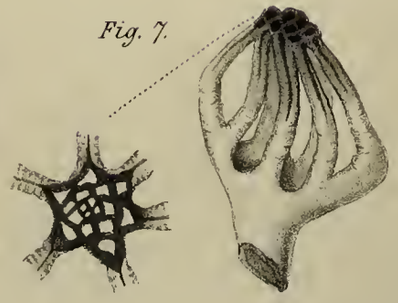

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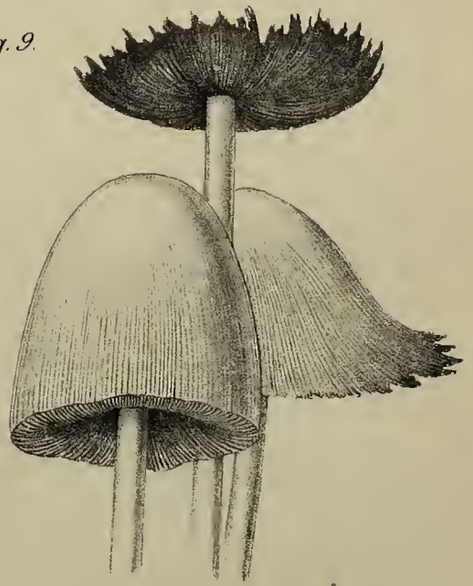


University Press, Oxford

On the Pitcher of Nepenthes: A study in the Morphology of the Leaf.

BY

F. ORPEN BOWER, D.Sc.,

Regius Professor of Botany in the University of Glasgow.

With Plate XVI.

THE ordinary method of morphological treatment of leaves is to distinguish from one another those parts, which can in very many cases be obviously recognised in the mature state with the naked eye, viz. the sheath, petiole, and lamina. This distinction of parts is commonly applied both in treating of simple and of branched leaves.

Those who have studied the development of leaves have for the most part followed in the same lines, and have pointed out how, as a rule, the primordial leaf is differentiated at an early period into two parts, viz. the 'foliar base' or sheath, and 'upper leaf' or lamina, while between these parts thus early distinguishable a subsequent process of intercalary growth results in the formation of the petiole. This method of distinction of parts is maintained by most writers on the subject, whether the leaf be a simple or a branched one.

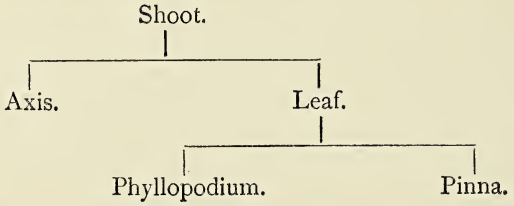
In a paper presented to the Royal Society in 1884[1], I pointed out that this method of treatment of the leaf is at variance with our treatment of the shoot as a whole: that in thus distinguishing sheath, petiole, and lamina, we lay stress upon the results of intercalary growth, which are regarded as only of

[1] On the Comparative Morphology of the Leaf, etc. Phil. Trans.

[Annals of Botany, Vol. III. No. IX. May 1889.]

minor importance in the treatment of the shoot as a whole; and we put on one side the branching of the leaf, though in treating of the shoot as a whole the time, place, and order of origin of leaves and buds upon the main axis are considered of primary importance, and indeed form the foundation of our morphology of the shoot at large.

Now, the fact that intercalary growth frequently obscures the branching of the leaf, does not appear to me to be a sufficient reason for sacrificing consistency of method; furthermore, a comparative study of the leaves of vascular plants low in the scale appears in no way to justify this sacrifice of consistency. I therefore proposed in the paper above mentioned, that in the morphological treatment of the leaf, the main axis of the leaf exclusive of all its branches should first be recognised, and distinguished as the *phyllopodium*, while the term *pinna* should be retained for the branches of the first order borne upon the phyllopodium. The relations of the parts of the shoot would thus be as follows:—



The practical difference between the two methods is this:—under the old method, placing the results of intercalary growth in the foremost place, we should, in attempting to solve a problem in foliar morphology, first ask, Where are the limits between sheath, petiole, and lamina? Under the method which I proposed, the first question would be, Does the leaf branch?

Finding that the method worked well in practice in ordinary cases, it was thought well to apply it to a familiar problematical case, viz. the pitcher of *Nepenthes*: the result is to suggest a new view as to its morphology. Previous writers (with the exception of Griffith) have assumed that this most wonderful

leaf is a simple, unbranched one, and the main question discussed by them has been, which part corresponds to the petiole, and which to the lamina of ordinary leaves? The chief views which have been advanced as to the morphology of the pitcher of *Nepenthes* are the following:—

(1) That the lid of the pitcher is the lamina of the leaf, while the rest of the leaf, including the pitcher itself, represents the petiole, which widens below into the broad assimilating expansion and basal sheath; this is the view held by Van Tieghem [1] and by Drude [2].

(2) Goebel [3], on the other hand, holds that the lid of the pitcher does not represent the whole lamina, but that it is only the upper end of the lamina, of which the pitcher is also a part. He would imagine the pitcher of *Nepenthes* as essentially similar to the bladder of *Utricularia*, and says, 'If we imagine the bladders of the latter greatly enlarged, the lid not folded over the inner margin of the mouth, but closing the wide opening like a lid, we should have the pitcher of *Nepenthes*.' He further regards the tendril as the result of intercalary growth from the upper limit of the petiole, the latter being represented by the broadly-winged basal portion of the leaf.

(3) It is to be noted that both these views ignore the fact, long ago demonstrated by Sir J. D. Hooker [4], that the apex of the lid is not the organic apex of the leaf, but that the latter is to be found in that spur which is constantly present in leaves of mature plants, immediately behind the point of insertion of the lid. Hooker, in the paper above cited, expresses the opinion that 'the pitchers are modifications of a gland situated at the apex of the midrib of the leaf'; he calls the lower flattened and winged part the lamina, and, speaking of the stalk of the pitcher, he says, 'It is a body more or less strictly analogous to the terminal cirrhus of the leaf of *Gloriosa* or *Flagellaria*.' He recognised what others who have written later failed to apprehend, that, 'as the pitcher enlarges, the apex,

[1] Traité de botanique, p. 1462. [2] Schenk's Handbuch der Botanik, i. p. 137.
[3] Ibid. iii. p. 238. [4] Linn. Trans. vol. xxii.

which points upwards and backwards, elongates at first considerably, and becomes the styliform process at the junction of the lid and the pitcher,' and that it 'continues to be the organic apex of the organ.' Further, he figures the peculiar bilobed conformation of the young lid, which leads me to the conclusion now to be put forward. In his Address at Belfast in 1874, he still maintains the view above quoted, and Eichler, in his paper on the leaves of *Cephalotus*[1], expresses his adherence to it.

Now, it is to be noted that these writers, under the influence of the old method, seek first to homologate the parts of the pitcher to sheath, petiole, and lamina,—parts which depend for their distinction upon the results of intercalary growth; and the question did not present itself to them, whether the leaf be a simple or a branched one. It was, however, a matter of the greatest interest to me to find the following passage written by Dr. Griffith in the year 1837[2]:—'There can be no doubt but that the pitcher is merely due to a hollowing of the apex of the petiole, or rather tendril. The lamina is of difficult explanation (if it is the lamina of the leaf) from its venation, its emargination, and the prolongated apex of the tendril; it is a compound one, analogous to the leaf of *Bauhinia*.' It will be seen that, though Griffith had apparently not made observations on the development of the pitcher, his comparison with the leaf of *Bauhinia* coincides in the main with the view to which study of the development of the leaf has led me.

My first observations were made upon a single bud of *Nepenthes*, sp. from Kew. These showed that the leaf first arises as a conical body, with the side directed towards the apex of the axis flattened (Fig. 1); the flattened side is soon marked by two longitudinal flanges or wings, while close to the apex a shallow oval depression soon makes its appearance. This is the first trace of the cavity of the pitcher (Fig. 2); above it is the smooth conical apex of the leaf, which is thus far a simple, winged phyllopodium. Subsequently the leaf elongates, the

[1] Jahrb. K. Bot. Gart. Berlin, i.

[2] Posth. Papers, vol. ii. p. 77.

wings increase, and a two-lobed outgrowth appears above the oval depression (Fig. 3, *p*); this is the lid of the pitcher, which, growing larger, ultimately covers the mouth of the cavity (Fig. 4). It will be seen in the examples to be described that the clearness of marking of the two lobes varies, even in the same species; but in the larger majority of cases it is clearly seen, and may usually be recognised even in the mature state; it was this that attracted Griffith's attention, and led him to suggest the comparison with *Bauhinia*.

Now, isolated observations, such as the above, upon the leaves from a single bud, are insufficient to settle the question of first origin of this two-lobed lid, and of its relation to the apex of the leaf. A comparison was therefore made of numerous leaves, in various stages of development, of *N. phyllamphora*, from the Glasgow Garden, and of *N. distillatoria* collected in Ceylon. In both these species the first stages are as above described. In *N. phyllamphora*, the lip of the oval depression becomes straight on the side nearer the apex (Fig. 5, *a*), while the apex itself becomes broad and flattened (Fig. 5, *b*). This is the first step in the formation of the lid, though the two lobes are not yet to be recognised; very soon, however, the flattening having increased, the apex (*ap*) and the two-lobed lid (*p*) are distinguishable (Fig. 6), becoming more clearly defined as the leaf grows older (Fig. 7). As before, the lid, retaining clearly its two-lobed character, covers over the cavity of the pitcher, while the growth of the apex frequently becomes irregular in this species, resulting in those variously laciniate spurs, which are easily recognised with the naked eye in the mature pitcher (Fig. 8). Meanwhile the part of the phyllopodium below the depression becomes differentiated into the pitcher itself (as Figs. 4, 8) and the basal expanded portion, while the intercalation of the tendril takes place subsequently.

Turning now to *N. distillatoria*, the results are in the main similar, the first stages being as before (Figs. 9, 10): the apex becomes flattened as seen in profile (Fig. 10), while the surface-view shows that the cavity is first overarched by a simple flap,

which represents the young lid (Figs. 11 and 13, *A*). The relation of the lid to the apex, which develops into the spur, is essentially the same as in *N. phyllamphora*, but it is only at a subsequent period that the two-lobed character of the lid becomes apparent (Figs. 14–17). The apex (*ap*) may in this species remain a simple cone, or it may occasionally assume an irregular form (Fig. 16), as is so frequently the case in *N. phyllamphora*.

It would be desirable to study the development of the pitchers in the first plumular leaves, and especially so after the interesting observations of Sir J. Hooker and subsequently of Prof. Alexander Dickson[1] on such leaves in the mature state. Unfortunately I have been unable to obtain specimens of seedlings in the earliest stages; I owe, however, to the kindness of Messrs. Veitch, of Chelsea, two of the youngest seedlings they could supply of *N. phyllamphora*. One of these had five, the other six expanded leaves; they were not so young as those described and figured by Hooker, though they were of such age that the tendril was not intercalated between the pitcher and the expanded base of the leaf, and the wings were obviously continuous from the base up to the pitcher. In the mature leaves of these young plants the spur was much less clearly to be recognised than in pitchers of more mature plants of this species, while the irregular fringes were larger in proportion than in older specimens; the lids were quite as clearly lobed as is usually the case in mature plants. Examination of the development of the leaves of these seedlings as exhibited in their terminal buds gave practically the same results as those above detailed for older plants, the relation of apex and lid, and the two-lobed character of the latter being quite similar. The evidence from these somewhat advanced seedlings cannot be regarded as conclusive, but as far as it goes it supports the view now to be put forward.

The above facts coincide in all essential points with the observations of Sir J. D. Hooker, and they lead me to the

[1] Proc. Roy. Soc. Edin. 1883–84.

following conclusion:—That the leaf of *Nepenthes* is not a simple but a branched one; regarding the spur at the back of the lid as the organic apex of the leaf, the lid which arises on its frontal or adaxial face, more or less distinctly below its extreme lip, and with a two-lobed form, may be regarded as representing two coalescent pinnae. The whole leaf would then consist of (1) a phyllopodium, winged throughout its length, terminating in the spur, and developing the pitcher itself as an involution of its upper surface; (2) a pair of pinnae, which show congenital coalescence across the frontal face of the phyllopodium, and constitute the lid of the pitcher.

I see only one other way of interpreting the facts. It might be possible to regard the lid as being truly the apex of the leaf, while the spur might be recognised as an outgrowth of the abaxial or lower surface of the leaf close to its apex, as in the leaf of *Iris*[1]; but against this view is to be set the difficulty of explaining the two-lobed character of the lid while young, its venation, and its emargination when mature without any trace of a central spine at its apex. Moreover, observation of stages of development, such as those shown in Figs. 5–7 and 10–13, though they do not show the point so definitely as might be wished, indicate, I think, plainly enough that the organic apex of the leaf is represented by the spur, while the lid arises on its adaxial surface, though very little below its apex. I therefore think that the latter interpretation of the facts is untenable.

Adopting then the view that the leaf is a peculiarly developed phyllopodium, bearing two pinnae which show congenital coalescence, it remains to draw comparisons with other leaves. I am not aware that any case exists of such coalescence of pinnae across the frontal or adaxial face of the phyllopodium. It is obvious that Griffith's comparison with the leaf of *Bauhinia* does not exactly fit. There the terminal spine, or true apex of the leaf, lies between the two pinnae, which are sessile upon the phyllopodium, being inserted upon

[1] Compare Goebel, Bot. Zeit. 1881, p. 96.

it by very broad bases; there is, however, in *Bauhinia* no extension of their growth across the adaxial surface. But if we pass on to stipules (which in many cases are without doubt essentially similar in their nature to pinnae, and may often be regarded as basal pinnae of peculiar character) similar developments are to be found. In the intra-petiolar stipules (e.g. of *Melianthus*) a coalescence of the two stipules across the adaxial surface of the phyllopodium has taken place, and such examples seem to approach most nearly to the constitution of the lid as above suggested for *Nepenthes*. It is to be admitted that the emargination of the lid is often very slight, while in early stages of development the lid may appear to be actually entire (Figs. 11, 13); but in this I see no grave ground for doubt of the assumed congenital coalescence. Numerous examples might be cited of congenital coalescence quite as complete as this, where the fact of coalescence is beyond doubt—for instance in the stellate *Rubiaceae*, and especially in *Rubia peregrina*, all stages of coalescence of the stipules may be found, from those in which the two stipules of one pair are united at their base, through those united for half their length, to those which show only two terminal teeth, but have two prominent midribs, and finally to such as are absolutely entire at the apex, and have only a single well-marked midrib. In these last the coalescence (which on comparative grounds cannot be doubted) is complete and congenital, and in them we have an example closely similar to the cases shown in Figs. 11 and 13. In the mature lids of pitchers the venation may, as in the above-cited case of *Rubia peregrina*, show a certain relation to the external form, and on looking over a number of specimens in Kew, it has been seen that, as a rule, where the emargination is distinct the venation is referable to the two lobes; while where the lid is most nearly entire there is frequently a single central rib more clearly marked than the rest. Similar observations may also be made on the coalescent pair of outer perianth-segments in *Cypripedium*. Other examples might be cited, but sufficient has now been said to show that the lid of the pitcher of *Nepenthes* presents in its

origin, as well as in its mature structure, characters which justify the conclusion that it is the result of a congenital coalescence of two pinnae.

Turning now to the phyllopodium, that is, the whole leaf exclusive of the pinnae which constitute the lid, the pitcher itself is seen to originate first as an involution of the frontal or adaxial face of it, near to its apex, and the involution begins before the lid makes its appearance. It is brought about by the more active growth in an area surrounding a certain point than at the point itself. In this respect the pitcher of *Nepenthes* corresponds to that of *Sarracenia* or *Utricularia*, while overgrowths of a similar order are not uncommon among other plants[1]. Dickson has compared the pitcher to the peculiar funnel-shaped, abnormal leaves of *Croton*, while Goebel has drawn the comparison between pitchers and orbicular leaves, and the pitcher may be regarded as an extreme instance of such slight hollowing of the upper surface as is to be found in such cases as *Hydrocotyle*, *Tropaeolum*, and *Nelumbium*.

Regarding then the pitcher as the result of involution of the upper surface of the phyllopodium at a point near its apex, it remains to consider the lower portion of the leaf. It has been pointed out in my paper above quoted that in very many cases, and especially in the Ferns, Cycads, and Dicotyledons, the phyllopodium is a winged structure throughout its length, and that those parts of it which may be distinguished when mature, depend for their differentiation upon the different mode of localisation of intercalary growth in them; the parts usually recognised may be termed the hypopodium (or sheath), the mesopodium (or petiole), and the epipodium (or upper portion of the main axis of the leaf exclusive of the pinnae); but in my former paper it was expressly stated (p. 610) that 'such distinctions are only to be drawn where they are warranted by the exigencies of description.' In simple sessile leaves it is obviously impossible to distinguish those parts.

[1] The tubers of orchids, and of *Phylloglossum*, and inferior ovaries; these, however, involve the actual apex, while here it is not the apex which is arrested in its growth, but the point of arrest is at some little distance below it.

Now, because certain modes of localisation of growth in the developing leaves are common, and since accordingly in large and complicated leaves the parts above distinguished usually have a certain conformation, it does not follow that this should always be the case. But the attempt made by most writers [1] to homologate the parts of such a peculiarly developed leaf as that of *Nepenthes* with the parts of leaves of the usual type, implies the assumption that it is possible to make the distinction in every case, and that the parts thus recognised are in some recondite way different from one another. In the absence of evidence that *Nepenthes* is descended from ancestors with a normal petiole, which in this plant became widened into its well-known expanded base, it will be well, I think, to give up the attempt to homologate the parts of this phyllopodium with those of the ordinary type. It was the unnatural extension of a generalisation, based on wide but not universal experience, to all cases, that ruined the spiral theory of Braun and Schimper; and in the case of the leaf the extension of the notion of transverse limitation must have like results. While we note that a distinction of petiole and lamina, as parts having usually a definite relation of form and position, is applicable to a large proportion of leaves, let us beware of assuming that the parts of *all* leaves, however peculiar their form, are referable to such a type.

To meet the difficulty of want of uniformity in different leaves, and especially in cases such as that now under discussion, it is, I think, important to fix the attention upon the phyllopodium throughout its length. It is, as a rule, a structure which is traversed by two longitudinal wings; such wings, or longitudinally directed flanges, are to be found in a very large proportion of leaves, from the lowest Ferns to the Dicotyledons, and, though not universal, the prevalence of this winged character is a much more constant and important phenomenon than those on which the distinction of sheath, petiole, and

[1] Drude and Goebel both attempt to define limits of petiole and lamina in *Nepenthes*.

lamina are based[1]. These wings are early recognisable in the developing leaf, and are usually present on its adaxial face; they are the seat of important subsequent growths; their most prominent mode of development is the formation of the lateral flaps of the simple lamina; or upon each of them may arise in longitudinal series the pinnae, which may remain rudimentary, and show congenital coalescence (as in leaves with serrate margins), or the pinnae may develop separately from one another (as in the truly pinnate leaf). The prevalence of these wings from the Ferns upwards, and the influence of their existence upon the ultimate conformation of leaves, makes it appear to me to be important to recognise their presence more fully than is usual; the recognition of the phyllopodium, as usually a winged structure, seems to me to lead to a better insight into the real nature of the leaf than the usual custom of drawing at once the transverse limitations of sheath, petiole, and lamina.

The phyllopodium, thus recognised, is susceptible of various development throughout its length, according to the varying balance of transverse and longitudinal growth. Where the transverse growth is relatively great, and the longitudinal less, the result is such a development as that which we usually term a lamina. Where the longitudinal growth is in the ascendant the result is what we call a petiole. Beyond the fact that these differences of localisation obtain respectively in those two parts, and that the petiole is intercalated at a relatively late period, there seems to me to be no essential or recondite

[1] This expression of opinion is diametrically opposed to that of K. Reiche (Ber. d. D. Bot. Ges., 1888, p. 328), who remarks as the result of the observation of winged *stems* and decurrent leaves of certain Phanerogams as follows:—'Dass die Flügel an pflanzlichen Organen aus geringen, morphologische Charactere darstellenden Bildungen hervorgegangen seien.' This conclusion is based on a narrow comparison. The author does not refer to any vascular Cryptogams or Cycads, and generalises from observations on a few stems to 'plant-organs' generally. Now the morphological importance of characters depends upon their prevalence through large groups, and the prevalence of a more or less clearly winged character in the leaf from the Ferns upwards is accordingly a character of morphological importance; certainly its importance in the *leaf* is not to be set aside because it is not prevalent or constant in the *stem*.

difference between petiole and lamina. Further, if this be the case, there is no need to assume that their order of succession on the phyllopodium shall be always the same: it is quite possible to imagine the balance of intercalary growth characteristic of what we call the lamina to be localised near to the base of the phyllopodium, while the intercalation of a part, comparable as regards its development to the petiole, may take place higher up; and this is exactly what takes place in *Nepenthes*, for the tendril-like prolongation is intercalated at the point marked (*x*) in Figs. 4 and 14. I would not go so far as to suggest the application of the term petiole to the tendril, and lamina to the expanded portion at the base, as this would be a use of established terms in a forced sense. It is, I think, preferable to drop the attempt to homologate the parts of all leaves to the usual plan as leading to unnatural comparisons, recognising, however, that the peculiar mode of development of the winged phyllopodium in *Nepenthes* shows in inverted order those characters which lead to the distinction of the parts usually termed petiole and lamina in ordinary leaves. It seems to me to throw no more light upon the morphology of the leaf of *Nepenthes* to call the basal expanded portion the petiole than it does to attempt to distinguish petiole and lamina in an absolutely sessile leaf: in other words, the terms petiole and lamina are to be used only in a descriptive sense, and it is not to be assumed that because such parts are commonly to be distinguished in leaves of complicated form, therefore the parts of all complicated leaves are referable to such a classification. In order to justify the use of the term petiole for the basal expansion of the leaf of *Nepenthes* it would be necessary to demonstrate that this plant was descended from a typically petiolate ancestor, and that the petiole had actually become transformed to the condition in which we see it; but such evidence is not forthcoming at present.

The above attempt to apply the method of treatment of the leaf, advocated in 1884, to a most problematical case has had the result of eliciting a new view of its morphology. The attempt has also shown that the method, which I believe to

be in accordance with our treatment of the shoot as a whole, is applicable to the most difficult cases. It is obviously an elastic method, and in this respect it accords with the morphological spirit of the time; it is generally recognised that in their adaptation to special physiological requirements plants are susceptible of the most varied development, and that this does not follow a rigid type. This is admitted as regards the arrangement of leaves on the shoot, in the branching of the shoot, and in the development of the nodes and internodes. It is time that, in considering the leaf, which is the most plastic of all members, a similar elasticity of method should be adopted, and the assumption that in complicated leaves the parts are necessarily referable to sheath, petiole, and lamina should be recognised as being based on insecure foundations.

December, 1888.

DESCRIPTION OF FIGURES IN PLATE XVI.

Illustrating Professor F. O. Bower's paper on the leaf of *Nepenthes*.

Nepenthes, sp.: Figs. 1–4.

Fig. 1. Apex of young leaf, *a*, with young leaf, *b*, seen in profile. × 36.

Fig. 2. Next older leaf of the same bud seen in full face; *c*, cavity; *w*, wings. × 36.

Fig. 3. An older leaf with the lid, *p*, already present; *ap*, apical spur. × 36.

Fig. 4. A leaf still older; *as*, the part which forms the pitcher; *xx*, the point of origin of the tendril. × 20.

Figs. 5–8, *Nepenthes phyllamphora*.

Fig. 5. Apex of stem, and young leaf; *A* as seen full face; *B* in profile. × 36.

Fig. 6. A somewhat older leaf; *ap*, apical spur; *p*, lid; *c*, cavity. × 36.

Fig. 7. Another leaf slightly older. × 36.

Fig. 8. A much more advanced leaf, showing irregular growth of the apex, *ap*. × 18.

Figs. 9–17, *Nepenthes distillatoria*.

Fig. 9. Young leaf in full face. × 36.

Fig. 10. Young leaf in profile. × 36.

Fig. 11. Apical portion of an older leaf in full face. × 36.

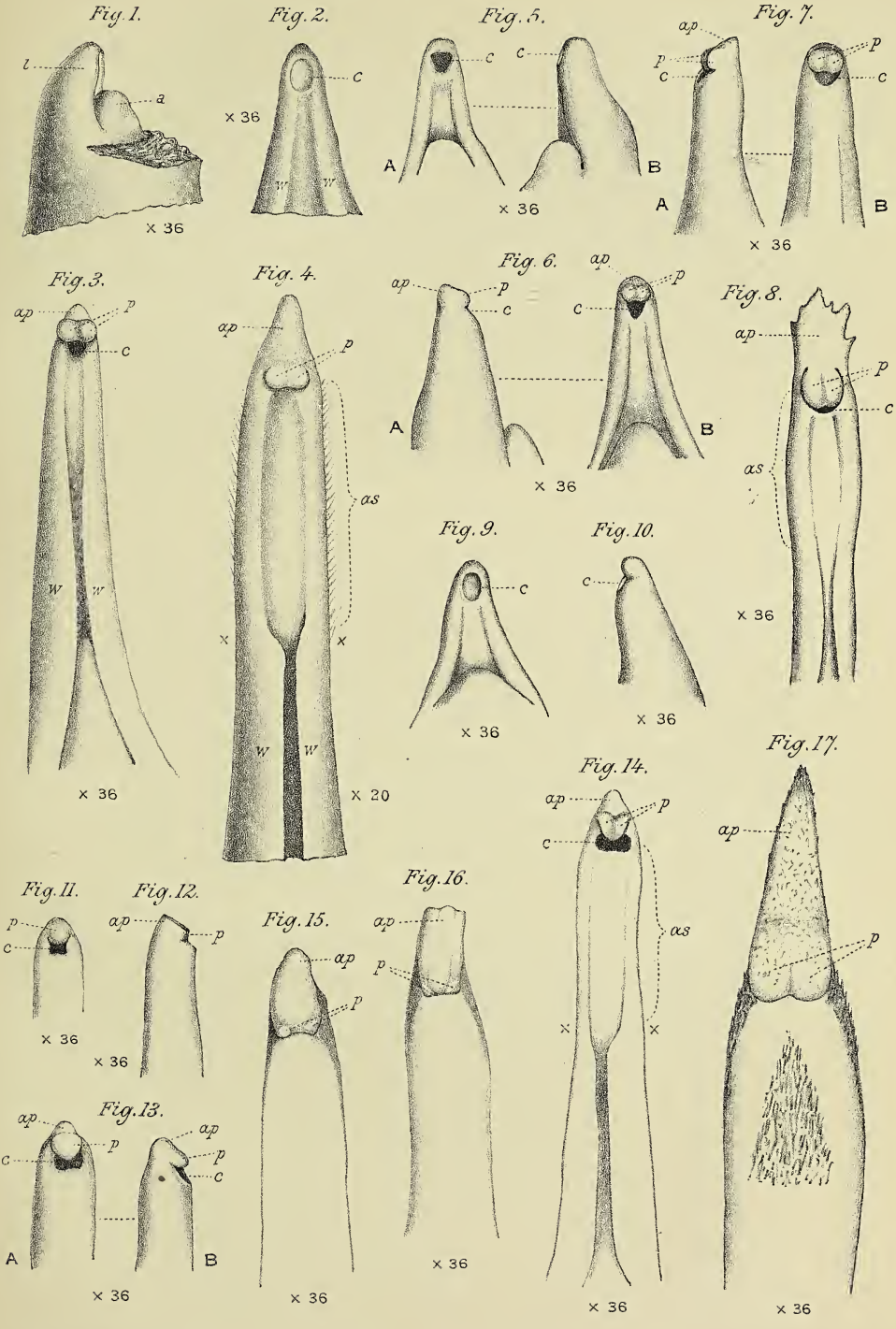
Fig. 12. do. do. in profile. × 36.

Fig. 13. do. do. in full face and in profile, somewhat older. × 36.

Fig. 14. A leaf more advanced; lettering as before. × 36.

Figs. 15–16. Leaves in which the lid has covered in the cavity of the pitcher. Fig. 16 shows irregular development of the apical spur. × 36.

Fig. 17. An older leaf of the same, showing very clearly the two-lobed character of the lid of the pitcher. × 36.



F. O. Bower del.

University Press, Oxford.

BOWER.—ON THE PITCHER OF NEPENTHES.

Observations on Pitchered Insectivorous Plants. (Part I.)

BY

J. M. MACFARLANE, D.Sc., F.R.S.E.

With Plate XVII.

Introduction.

THE following observations were begun in the autumn of 1884, and most of the anatomical details were worked out by the middle of 1885. I gave in 'Nature' (25th December, 1884) a short general account of my earlier results. After its appearance I was able to work out the subject in considerable detail, but for various reasons the publication of my completed research has been greatly delayed, though I presented a general epitome of it at two meetings of the Royal Society of Edinburgh in the summer of 1885.

A dissertation thesis was published by Zipperer[1] in May 1885, in which he confirmed some of my results which had previously appeared in 'Nature.'

Five genera of pitchered insectivorous plants are at present known, viz. *Nepenthes*, *Heliamphora*, *Sarracenia*, *Darlingtonia*, and *Cephalotus*. All of these, except the second, have been in general cultivation for years. *Heliamphora*, described by Bentham in 1842[2] from dried specimens, has recently been introduced from Mount Roraima by Mr. Veitch of Chelsea, and through his kindness I have been able to examine fresh specimens.

[1] Beitrag zur Kenntniss der Sarraceniaceen. München, 1885.

[2] Trans. Linn. Soc. XVIII (1842).

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In this paper I will present my results under the following heads:—

1. General morphology of the pitchers.
2. Histology of *Darlingtonia*, *Sarracenia*, and *Heliamphora*, with remarks on adaptations for insect catching.
3. General morphology and histology of the flowers of these.
4. Arrangements for pollination in the flowers of *Sarracenia*.
5. Histology of *Nepenthes*, with remarks on adaptations for insect catching.
6. General morphology and histology of the flowers of *Nepenthes*.
7. Arrangements for pollination in the flowers of *Nepenthes* and *Cephalotus*.
8. On hybridity and relation of the species to each other in the different genera.

Ordinary methods were adopted in sectioning and mounting. For the obtaining of large epidermal surfaces showing the relative distribution of glands a special method was adopted [1]. The pitchers were macerated in strong boiling potash solution, and this, though destroying the cuticle, gave large transparent pieces in which the form of ordinary epidermal cells, gland and hair cells, was well illustrated.

I. General Morphology of the Pitchers.

Professor Dickson has fully elucidated the morphology of the *Cephalotus* pitcher [2], so that I only require to draw attention to the flowers of that genus in a later part of my paper.

NEPENTHES.

This genus, though highly specialised both in leaf form and glandular development, is the one which may most conveniently be examined first. In all the known seedlings of

[1] Brit. Assoc. Report. Aberdeen, 1885.

[2] Journ. of Bot. N.S. Vol. VII (1878); also Vol. X (1881).

Nepenthes the leaves produced immediately after the cotyledons have the lamina gradually expanded from below upwards, and towards the apex the margins of the laminar lobes curve round and fuse with each other in front of the pitcher (Plate XVII, Fig. 1). The tissue of the midrib in the upper half of the lamina opens out to form an elliptical and slightly bellied area on the dorsal[1] or upper leaf-surface view. This expanded dorsal midrib area is therefore bounded all round by the fused laminar lobes. The pitcher at this time appears as a ventral pouch-like cavity, adnate to the under surface of the lamina, and with its orifice projecting beyond the fused laminar lobes. A lid springs from the ventral side of the orifice, and from its junction with the pitcher a small filamentous process projects. This has been regarded by all writers on the subject as the organic leaf apex, and to this view I adhere.

But to understand rightly the relation of parts in *Nepenthes*, as well as in the other genera to be treated of, we must examine the vascular distribution. The vascular bundles of the midrib about the middle of the leaf begin to open out to form the framework of the pitcher. Two bundles, gradually diverging from each other on the dorsal side, run round and form the boundary of the bellied laminar area already mentioned. Like the lamina these bundles, by forming anastomosing branches, fuse at the apex in front of the pitcher. As they run upwards they give off vascular branches, some of which spread out over the bellied area, and ultimately anastomose with each other along its middle. Other branches run into and traverse the laminar lobes, while the strongest of all are those spreading out along the lateral and ventro-lateral surface of the pitcher. The remaining bundles of the midrib run up the ventral part. The lateral and ventro-lateral branches of the two bundles, when they approach the orifice of the pitcher, curve round to the ventral side, and there unite with the ventral bundles to form the projecting filamentous

[1] Dorsal and ventral are used throughout in the sense of the leaf being a dorsiventral structure.

apex, after they have given off two strong diverging branches into the lid.

As older leaves are produced certain important changes occur. The lamina at the level of the pitcher bottom becomes constricted, until separation into two flat basal lobes, and two terminal ones is effected, the latter appearing as flap-like projections from the dorsal side of the pitcher; and in this genus they continue to remain widely separated laterally, since the two bundles, previously mentioned, retain their position (Fig. 2). Further, owing to encroachment of the corrugated pitcher-rim the dorsal laminar fusion is gradually reduced till, in most adult pitchers, it is unrecognisable. But while its presence is occasionally represented as a ridge-like elevation in some species (e. g. *N. Khasiana*), in all species branches of the two bundles still curve round to meet each other in front of the pitcher. Therefore, though the fused laminar parts may be reduced or disappear, their vascular supply is still represented by these bundles. Clearly then we have here to deal with two leaflets which become fused or connate in front of the pitcher. But it is interesting to note that in a few species (e. g. *N. Rajah*) the basal lobes likewise become beautifully connate at their apex by union on the upper or dorsal side of the midrib, and an inclination to similar fusion of the basal lobes is observable in many species.

Before discussing the lid and filiform apex, I may refer to the mode of development of adult pitchers as described and figured by Hooker[1]. The late Professor Dickson also kindly allowed me to examine a series of preparations which he had made.

Each leaf arises from the axis as an elongated protuberance, and soon shows on the dorsal side a basal concave area bounded by a continuous ridge, and near the apex a dimple-like depression separated from the concave area by the transversely-placed part of the ridge already mentioned. The concave area corresponds, I consider, to the uninterrupted lamina of the seedling pitcher. But as the leaf grows it

[1] Trans. Linn. Soc., Vol. XXII (1859).

follows the line of development taken by the seedling leaves, in that the concave area separates into a basal midrib portion, whose bounding ridges grow out to form a pair of laminar lobes, and an upper midrib portion whose bounding ridges become the wings of the pitcher, while deepening of the dimpled depression behind these lobes gives rise to the pitcher cavity.

But the extreme leaf-apex projects from the first beyond the depression as a rounded mass. This, as development proceeds, gives rise either to one ventral median swelling which grows forward and downward over the cavity, or—as figured by Hooker in *N. phyllamphora*—two swellings may appear, one on each side of the middle line. By continued growth of the former, or by fusion and growth of the latter, the lid is formed.

The terminal part of the leaf apex may further give off from its side paired filamentous lobes, or a single dorsal lobe in the middle line, though a rather irregular disposition also occurs. They are by no means conspicuous, but I regard them as of special morphological interest.

When the lid and filiform apex are fully grown, one finds that, just as in the seedling, the vascular bundles of the pitchered midrib which have converged give off two strong diverging bundles into the former, then pursuing their course upward they give off very delicate branches into the lateral or median lobes, and finally merge into cellular tissue of the extreme tip. It should also be noted that the adult lid in some species shows a slight tendency to division or indentation at its free extremity.

How then are we to explain the lid and filiform apex with its delicate lateral or median lobes. First, I think, it may be conceded that the converged bundles at the top of the pitcher truly represent the midrib of the leaf reformed or recompacted after being inflated to receive a dorsal involution of itself—the pitcher.

One almost hesitates to give it so peculiar an explanation, but I can scarcely see that the lid is to be regarded otherwise

than as the result of an exaggerated dorsal fusion of two originally lateral leaflets. Various weighty reasons may be urged in favour of this view. As we have already stated, the lid in some species arises as two lobe-like processes which ultimately fuse. In adult lids the free extremity may be more or less indented; also two strong diverging vascular bundles come off from the recompacted midrib. Further, if we compare the supposed condition here with other leaf-fusions, we shall discover that it is not a peculiar one. Thus the fused or connate axillary stipules of various orders of plants originate exactly in the way that we imagine the lid of *Nepenthes* to do. Both are foliar parts which, growing round dorsally, fuse to form a median laminar process. Again, another parallel is seen in connate leaves, for if we suppose two connate leaves to develop entirely on the axillary or dorsal side of their supporting branch, i. e. dorsally instead of bilaterally, they will by fusion appear as a projecting leaf growing towards the main axis, and traversed by two midribs. But I think that a highly important confirmation of the above view is to be had in the presence of paired lateral or unpaired median lobes on the filiform midrib extremity *beyond* the point of origin of the lid. A feature which at first sight goes against the view just propounded is exhibited in pitchers of *N. Veitchii*, etc., where a strong ridge-like thickening occurs on the inner lid surface in the median line. But when examined microscopically this is seen to consist merely of cellular tissue, and is of no morphological importance. It need scarcely be added that the xylem of the lid bundles lies facing the pitcher cavity, while the phloem is directed upwards, though this is an additional confirmation of the above.

We may fairly view a *Nepenthes* leaf then as being compound and composed of from 3 to 4 or 5 pairs of leaflets disposed along a midrib, and that both leaflets and midrib undergo striking modifications, the leaflets in particular showing a marked tendency to dorsal fusion above. In Plate XVII, Fig. 7, I have given an ideal diagram of an entire leaf of *N. Rajah*. First, the basal part of the midrib carries two elongated green

leaflets showing dorsal fusion in their upper region; second, the midrib is prolonged as a tendriliform structure; third, the midrib opens out to receive a dorsal involution of itself from above, and carries on its sides two wing-like leaflets showing dorsal fusion distally; fourth, above the involution the midrib carries two leaflets which by an exaggerated dorsal fusion form the lid; fifth, the midrib now reduced to a filiform process may next give off two very small lateral leaflets; sixth, it may produce a dorsal median process which probably represents two lateral leaflets with dorsal fusion. The midrib then runs out into a fine point.

The mode of formation of the corrugated margin is easily explained. It results from flattening out of the orifice rim externally and internally and curving over of each upon itself. The remarkable species *N. Lowii* (for pitchers of which I am indebted to the kindness of Mr. Burbidge, of Trinity College Gardens, Dublin, and Mr. Veitch of Chelsea) retains, as I will point out more in detail afterwards, the primitive condition of a simple rim, and the marginal glands of Dickson are disposed round it with exposed orifices, the whole being beautifully illustrated in Hooker's figure of the species [1].

HELIAMPHORA.

This is a genus of low growing plants and includes only one species, *H. nutans*, which forms rosettes of leaves close to the ground. These having no need of supporting tendrils may be said in some respects to remain permanently in the condition of seedling *Nepenthes* leaves. If a young leaf one or two inches in length be examined it will be seen that in it, as in *Nepenthes*, there is a basal portion consisting of a solid midrib with lateral laminae; in both the midrib vascular tissue then spreads out to form the framework of the pitcher cavity; here also the front of the pitcher has two continuations upward of the basal lamina which project as two dorsal wings. Most of the vascular tissue also which has opened out curves round

[1] Trans. Linn. Soc., Vol. XXII (1859).

or runs straight up and again fuses into a recompacted midrib at the top of the pitcher. But the two genera differ in that the basal laminae of *Heliamphora* remain permanently as undivided lobes, also the dorsal area between them and in front of the tube is reduced to a line so that the wings are thus brought close together and their surfaces stand out from each other at an angle of about 90° in seedling leaves, and nearly in line with each other in the adult. As we shall shortly see, the possession of these structural details causes *Heliamphora* to take a position intermediate between *Nepenthes* on the one hand and *Sarracenia* or *Darlingtonia* on the other, and this is further confirmed by the relative complexity of its glandular tissue. The lid, which in seedling leaves closely resembles that of *Sarracenia rubra* will be best understood after we have examined that genus. In Fig. 4 I have drawn a seedling leaf for comparison with that of the other genera.

SARRACENIA.

Like the last this is a genus of low growing plants producing similar rosettes of leaves. Six distinct species are known and in cultivation, *S. flava*, *S. Drummondii*, *S. rubra*, *S. variolaris*, *S. purpurea*, and *S. psittacina*. A. de Candolle[1] enumerates another two species, *S. Sweetii* and *S. undulata*, of which I can learn nothing. All the species, though differing considerably in form, colouring, and histological details, exhibit fundamentally the same morphological type of leaf, and the leaves may or may not show pitchering of the midrib. *S. flava* and *S. Drummondii*, have pitchered and arrested leaves (Fig. 8) nearly in equal proportion; the remaining four produce only or mostly pitchered leaves.

Very diverse views have been advanced to account for the leaf form in the genus. St. Hilaire and Ducharte viewed the leaf as a pitchered petiole crowned by a lid representing the true leaf. Baillon[2], after tracing the development of it, com-

[1] Prodromus, Vol. XVII (1873).
[2] Comptes Rendus, LXXI.

pared it with a peltate *Nelumbium* leaf, and concluded that the lower solid part is the petiole, the pitchered part the leaf bearing on its front or dorsal side a flap-like excrescence comparable, he considered, to a ridge often seen on the outer base of peltate Nymphaeaceous leaves, while the lid represented a terminal leaf lobe. Asa Gray considered that 'they are evidently phyllodia' and looked upon the lid as the leaf blade. For he says 'in *S. variolaris* the hooded summit answering to the blade of the leaf arches over the mouth.' I will now try to show that a more natural and correct explanation can be given, one also in consonance with the other three genera. I have gone over the development of the adult leaf and find that, as in *Nepenthes*, each grows out at first as a little cone with concave basal part and rounded apex, below which a depression is formed. But even in very young leaves, between the concave area and slit-like depression a median ridge arises, which, as the leaf grows, gets greatly enlarged (Fig. 9 *a*). If the leaf becomes pitchered the cavity is formed in the midrib above the ridge, if it fails to pitcher the ridge develops as a large laterally compressed outgrowth of the midrib, and towards the apex it gradually curves into the midrib. Just beyond the point where it ceases a minute slit-like depression can be detected, so that, though some of the leaves of *Sarracenia* may fail to produce a pitcher, they nevertheless show the rudiment of it. The basal depressed area becomes the leaf-sheath which is always strongly concave, while its bounding ridges become two rudimentary but very evident lateral lobes growing out from it. These gradually converging run face to face with each other and merge into the solid midrib above. But their applied faces are directly in line with the upper median wing, and a delicate groove continuous from the middle of their applied faces runs upwards on to the middle of it. I will now try to prove that this ridge is produced by fusion of what in *Nepenthes* are the widely separated dorsal flaps, and in *Heliamphora* the closely applied dorsal flaps. The leaf-sheath with its rudimentary lobes corresponds to the large green basal leaflets of *Nepenthes*,

the solid midrib above corresponds to the tendriliform midrib of *Nepenthes*. Now, if a section of a pitchered *Sarracenia* leaf be made a little higher than the pitcher bottom, and microscopically examined, one sees (Fig. 12) that a cylinder of bundles surrounds the cavity, but that the wing or dorsal flap has two rows of bundles parallel to, and with their xylem facing each other. This can only be explained on the supposition that we have here to deal with opposite leaf lobes whose faces are not only applied to each other but organically fused. After noticing this I turned to the leaf of *Iris* for verification, since it has long been known to exhibit such a condition. The exact agreement of the two in fundamental structure will be demonstrated by reference to Figs. 12 and 13. The only slight difference is that while *Iris*, like most Monocotyledons, has a feeble, practically unrecognisable midrib, in our genus it is very large. The tubular pitcher therefore is the hollowed-out upper part of the midrib, and the dorsal flap growing out from it results from fusion of two leaflets.

The lid in the different species varies considerably. In *S. flava*, *S. Drummondii*, and *S. purpurea*, one strong median ventral and two feebler ventro-lateral bundles, after traversing the pitcher, tend to converge without fusing, while they are joined by transverse branches. These, along with still feebler bundles which join them after circling round the orifice, all give off lateral veins into the expanded lateral lobes of the lid. In *S. rubra* five bundles of the pitcher run straight up into the lid, the two lateral ones being joined by small bundles from round the orifice. In *S. variolaris* and *S. psittacina* the median ventral bundle is very strong while two to four feeble lateral bundles join it. In all cases then the pitcher bundles tend more or less to recompact themselves, and after entering the base of the lid give off radiating branches. I think we may therefore rightly regard the lateral lobes of the lid as a pair of leaflets given off from a midrib which does not, as in *Nepenthes*, pass off into a filiform process, but is continued upward between the lobes as an expanded median plate.

Additional reasons can be advanced in favour of this. Thus in *S. flava*, the strong median bundle after being joined above the level of the middle of the lid by the lateral bundles runs up, and before reaching the extreme top of the lid passes off as a filiform process. The extremity of this process in large leaves exhibits a peltate or cuplike cavity abundantly studded with honey glands (Fig. 10). We have here, therefore, an undoubted approach to terminal fusion of leaflets such as gives rise to the lid of *Nepenthes*. Again, in those leaves of *S. flava* and *S. Drummondii* which do not pitcher, the midrib always ends in a simple curved spur (Fig. 8), just beyond the depression which has been arrested in its attempt at pitcher formation. Were the lid merely an expansion of the midrib and not composed of leaflets we should at times expect to see the rudiment of it formed at the sides of the curved spur. This I have never observed. But the most interesting conditions to my mind are those presented by *S. variolaris* and *S. psittacina*. In the former the upper part of the pitchered midrib arches over the orifice and thus becomes convex, a little higher a constriction from side to side occurs, beyond this the lobes of the lid enlarge and become strongly convex, while their upper parts form two rounded projections on each side of the midrib, so that the lid resembles a convex emarginate leaf.

In *S. psittacina* the leaves all lie parallel to the ground with their dorsal flap uppermost. The top of the pitcher overarches very strongly and then contracting bounds a small orifice, so that the leaf in appearance exactly resembles that of *Darlingtonia* without its bilobed lip. On more careful examination one finds that the vascular tissue of the pitchered midrib becomes compacted and terminates in a slightly curved point considerably above (natural position), i.e. further removed ventrally from, the orifice than the actual margin, and that a dorsal laminar outgrowth from this forms the upper pitcher margin (Fig. 11). This is a repetition then of the condition of *Nepenthes* lid, and the two only differ in the relative width of their attachment to the midrib which gives origin to them. But

this dorsal downgrowth from the leaf apex in *S. psittacina* undoubtedly corresponds to the bilobed lip of *Darlingtonia*, so that, though *S. psittacina appears* to have no part corresponding to the lip of the latter, a cursory examination will prove that the two parts in question are the same.

The genus *Sarracenia* then shows in a fully developed leaf a pair of basal sheathing leaflets of a delicate white or greenish white colour growing from the front of the midrib, a solid midrib prolongation destitute of lamina, at least for some distance, a pitchered midrib portion in front of which two elongated green leaflets have fused producing a prominent wing, a dorsal continuation of the pitchered midrib in flattened form which gives off on either side two leaflets, the whole constituting the lid, and finally, in some species, a filamentous midrib termination, which, by possession of a terminal peltation, may indicate the incipient production of an additional leaf part.

DARLINGTONIA.

This genus is monotypic, *D. californica* being found in swamps in the Rocky Mountains. It agrees in habit with the two last genera. Having studied *Sarracenia*, the only part which calls for further notice is the leaf extremity. The ventral and ventro-lateral parts of the pitcher are greatly developed here in an overarching manner, and the associated vascular bundles, after ramifying over the arched portion, converge in the middle of the outer or ventral rim of the orifice. From this point the bilobed flap hangs as a dorsal development, and is abundantly supplied with vascular tissue. I have not been able to trace the number of bundles entering it at its attached base, but several sets radiate out in a bilateral manner on each side of its middle line, and these apparently result from branching of a smaller number at the base. The exact homology of it with the lid of *Nepenthes* is evident, but it also corresponds, as already noticed, to the area in *S. psittacina*, intervening between the organic leaf apex and the pitcher orifice on the ventral side.

CEPHALOTUS.

The pitchers of this genus appear to differ in every respect from those just passed under review, so that no comparison of them can be made. As Dickson clearly showed, the pitcher is a laminar involution, while the lid is a flap of the lamina growing forward over it. Like many other Australian plants therefore it seems to represent one of a chain of forms otherwise lost to us.

To tabulate briefly the foregoing conclusions we may say :—

I. That the leaf in *Nepenthes*, *Heliamphora*, *Sarracenia*, and *Darlingtonia* is compound, and consists of from two to five pairs of leaflets.

II. That a marked tendency to dorsal fusion of the leaflets from apex to base is shown.

III. That in seedling leaves of *Nepenthes*, and in seedling and adult leaves of *Heliamphora*, one pair of leaflets is continuous from the leaf-base up to the orifice of the pitcher, but that in adult *Nepenthes*, as also in *Sarracenia* and *Darlingtonia*, these separate into two pairs of leaflets, one pair being basal, and forming either elongated green laminae (*Nepenthes*) or membranous sheaths (*Sarracenia* and *Darlingtonia*). The upper pair is either continued up the front of the pitcher as two widely separated flaps which fuse distally (*Nepenthes*) or by close approximation and fusion of their faces they become a median dorsal wing (*Sarracenia* and *Darlingtonia*).

IV. That the pitcher is a deep dorsal involution of the midrib just above the termination of the fused upper pair of leaflets.

V. That the lid is made up of two leaflets produced on either side of a median midrib, which may afterwards be excurrent (*Heliamphora*, most species of *Sarracenia*), or the leaflets may fuse distally to form a median dorsal process, the midrib either passing off as a filiform process from which other leaflets of a rudimentary nature spring (*Nepenthes*), or terminating in an abrupt point (*S. psittacina* and *D. californica*).

EXPLANATION OF FIGURES IN PLATE XVII.

Illustrating Dr. J. M. Macfarlane's paper on Pitchered Insectivorous Plants.

Fig. 1. Seedling *Nepenthes* leaf. *a*, petiolar sheath. *b*, basal laminar lobes. *c*, upper laminar lobes.

Fig. 2. Seedling *Nepenthes* leaf, older than last. *d*, lid.

Fig. 3. Semi-diagrammatic representation of Fig. 2 for comparison with Figs. 4, 5, and 6.

Fig. 4. Seedling leaf of *Heliamphora nutans*.

Fig. 5. Seedling leaf of *Sarracenia rubra*. *ab*, reduced petiolar sheath and basal laminar lobes.

Fig. 6. Seedling leaf of *Darlingtonia californica*.

Fig. 7. Diagrammatic view of leaf of *Nepenthes Rajah*. *a*, petiolar sheath. *b*, basal laminar lobes. *ba*, prolonged tendriliform midrib. *c*, upper laminar lobes attached to, and fused together at the top of the pitchered continuation of *ba*. *d*, fused pair of leaflets forming the pitcher-lid. *e*, median process growing out from the filiform midrib extremity. *f*, pair of similar processes representing reduced leaflets. *g*, apex of leaf midrib.

Fig. 8. Leaf of *Sarracenia flava* which has failed to pitcher fully. *ab*, petiolar sheath and basal laminar lobes fused distally. *c*, midrib with dorsal wing resulting from organic union of two leaflets by their upper surfaces. At the curved apex a slight depression is present representing a rudimentary pitcher.

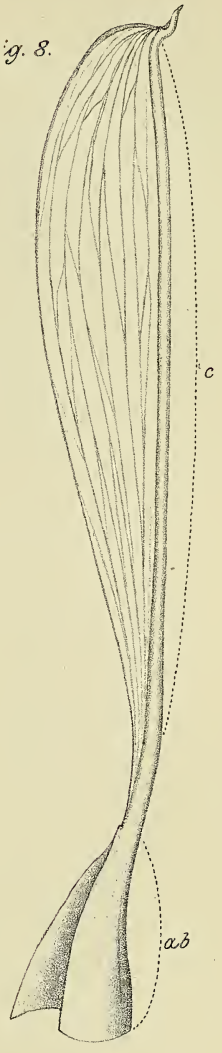
Fig. 9. Development of *Sarracenia flava* leaf. 9 *a*, earlier stage showing sheath and ridge. 9 *b*, later stage with pitcher depression appearing above median ridge. × 5.

Fig. 10. Upper part of *Sarracenia flava* lid, showing excurrent midrib, *m.r.c.* and fusion of lid leaflets beyond excurrent point.

Fig. 11. Upper leaf part of *Sarracenia psittacina*.

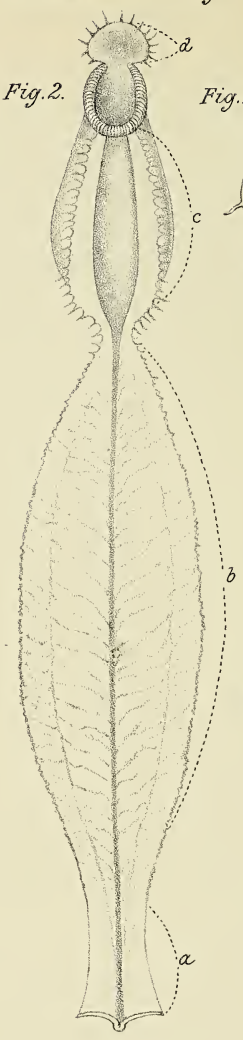
Fig. 12. Transverse section of *Sarracenia flava* leaf slightly above level of pitcher bottom. The fibro-vascular system alone is represented. *p*, pitcher cavity. *x*, double row of bundles of dorsal wing. *xyl. t*, fibres on inner side of xylem. *xyl. v*, vessels of xylem. *phl*, phloem. *phl. t*, fibres on outer side of phloem. × 30.

Fig. 13. Transverse section of *Iris germanica* leaf. Lettering as in last. × 10



University Press, Oxford.

Fig. 2.



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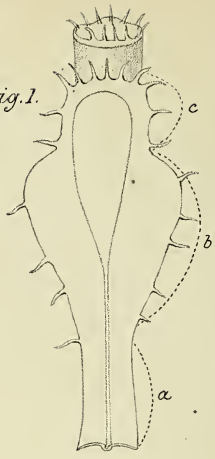

Fig. 3.

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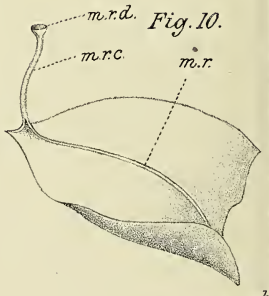
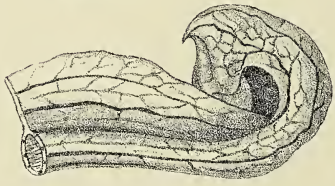


Fig. 12.

Fig. 11.



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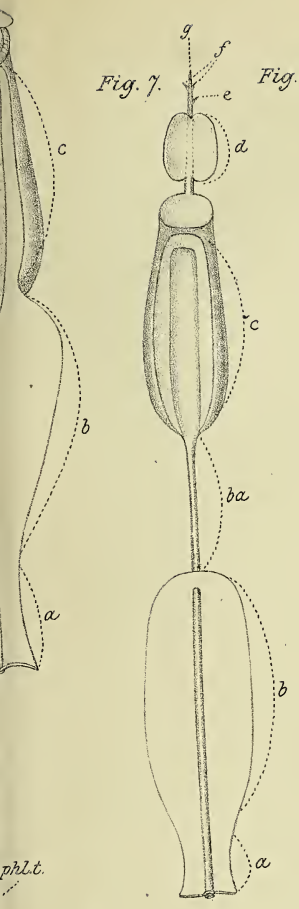
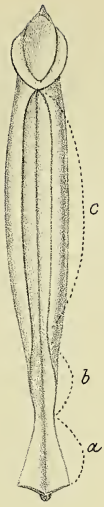


Fig. 7.

Fig. 4.



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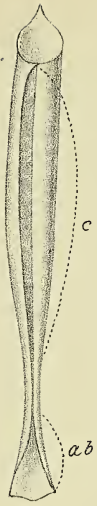

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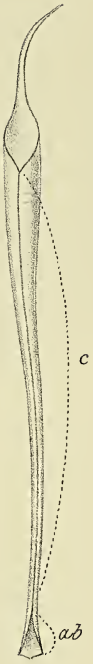

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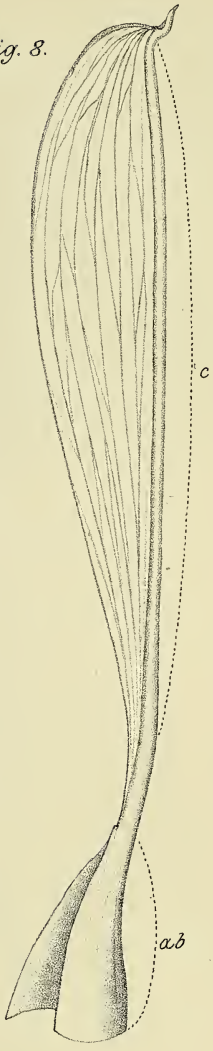

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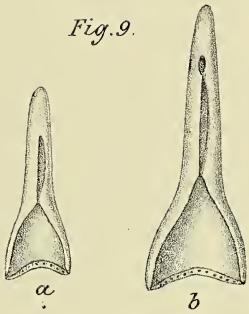

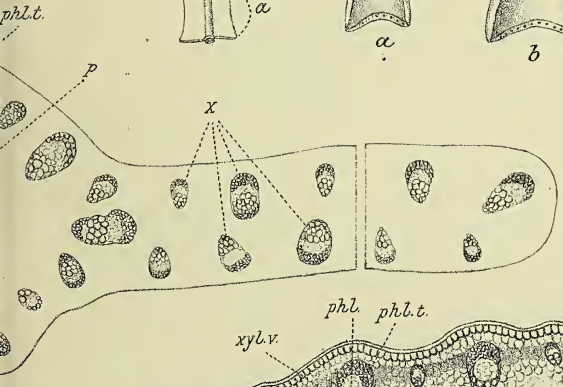

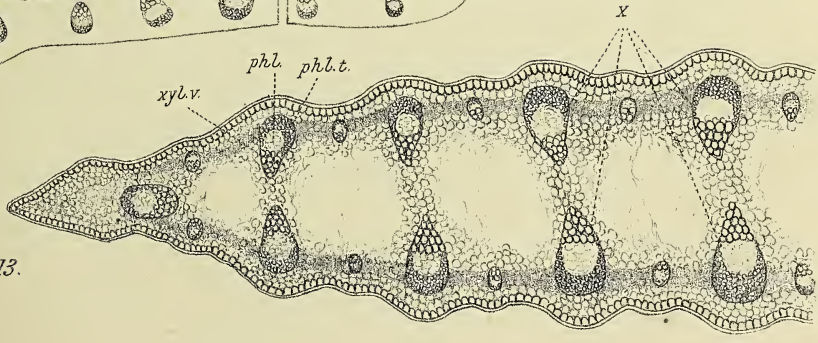

Fig. 13.

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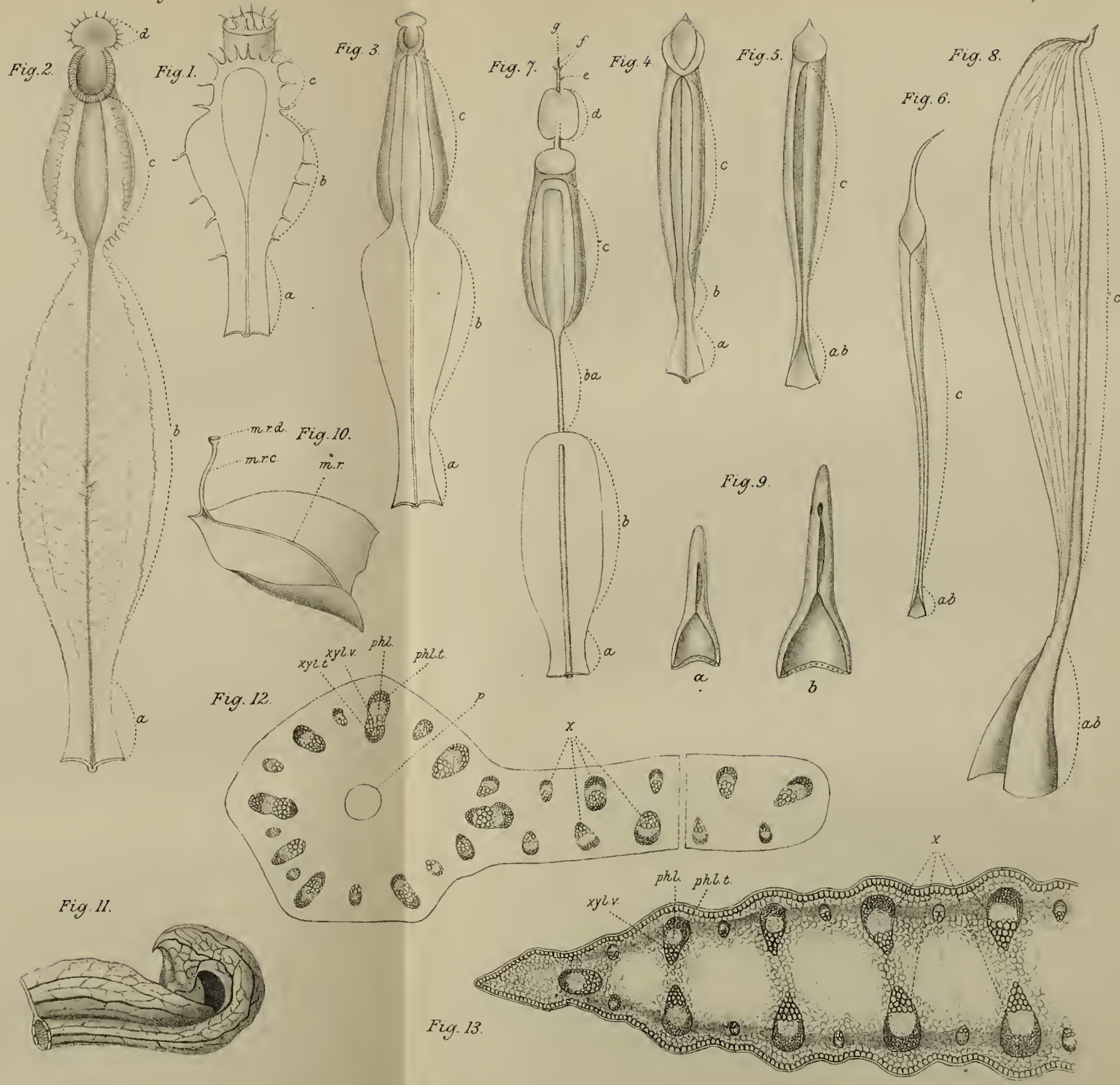
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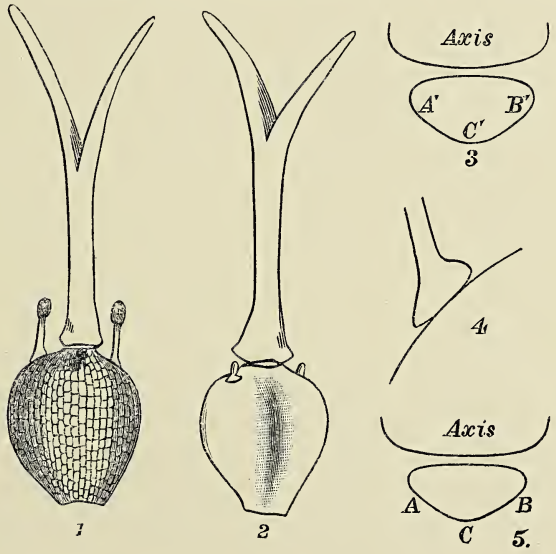
x

NOTES.

AN ABNORMAL EPIGYNOUS CYPERACEA.—There is in the Berlin Herbarium a good example of *Fimbristylis cymosa*, R. Br., collected in the Radak Isles (Chamisso n. 148). Fig. 1 shows one nearly ripe (black) nut of this, with three staminodes on the top of the nut. Fig. 2 shows another nut with two very minute rudiments corresponding to the two larger staminodes in Fig. 1. The staminodes in Fig. 1 are white or pale yellow, resembling the tissue of the filament in the full stamens; the (supposed) rudimentary anthers are fuscous black; they afford only a suggestion of being two-celled.

In the Scirpeae the stamens are often three or two in the same spikelet; Fig. 5 is the ground plan of a normal flower; the two stamens *A*, *B* belong to the interior whorl; the third stamen *C* is of



the outer whorl (in many large Scirpi it can be easily seen to be exterior to, and attached lower down on, the axis than the other two), and it is this stamen of the outer whorl that is often suppressed.

The position of the staminodes in Fig. 1 and Fig. 3 corresponds to that of the three stamens in the normal case, and the smaller size

and occasional suppression of *C'* adds great force to the argument that they are really staminodes.

There is some difficulty, however, in supposing that the staminodes represent stamens accidentally confluent with the pistil; Fig. 4 shows (more enlarged) the manner in which the white base of the rudimentary filaments sits upon the shoulder of the nut, as if a trichome.

There are no proper stamens attached to the two nuts figured, but in nuts so ripe they might have fallen.

C. B. CLARKE, Kew.

ON MACROSPORIUM PARASITICUM.—In the spring of 1887, at the request of the Secretary of State for the Colonies, I went to the Bermuda Islands for the purpose of studying a disease at that time very prevalent among the onion-plantations of that colony. I had been informed that the trouble was caused by the attack of an injurious insect, and consequently I was, on my arrival in Bermuda, rather disconcerted to find that the disease was obviously due to a parasitic fungus. Owing to the difficulty of communication with the mainland, and the scarcity of scientific works in the hands of the American booksellers, I was unable to procure any literature on the subject of parasitic fungi, and so was thrown entirely on my own resources to work out the life-history of the fungus causing the disease amongst the onions. At the very beginning of my investigation I found that the disease had two stages: the first, which the planters called the white mildew, was caused by the *Peronospora Schleideniana*, and was described by me in the Kew Bulletin, No. 10. The second stage is caused by *Macrosporium parasiticum*, and it appears in Bermuda only upon those plants which are dead or dying, having been killed by the *Peronospora*.

I made a number of very careful drawings of all the stages of the life-history of the *Macrosporium* which I could procure, in the very primitive laboratory I established at Hamilton. I was, however, unable to work out the development or the structure of the perithecium, and therefore I have never published these. The publication of the able paper 'On the life-history of *Macrosporium parasiticum*' by Mr. Kingo Miyabe[1], however, cleared up these points, and in this note I propose only to point out a few details in which his observations

[1] Annals of Botany, No. IX, 1889.

differ from mine, and to describe the naked-eye appearance of the infected plants.

After the plant has already been weakened by the *Peronospora*, the *Macrosporium* makes its appearance as patches of a dense black colour and velvety appearance. The patches gradually spread, forming belts an inch or more in width round the leaf. This dense black appearance is followed by a fluffy white growth, which stands out from the leaf for the distance of one-tenth of an inch. This is caused by the hyphae which grow out of the multicellular spores. Whilst the *Macrosporium* is growing, the leaf continues to rot; it does not shrivel and dry up as it does when attacked only by the *Peronospora*, but the plant retains a great deal of moisture, is very slimy, and gives rise to a most offensive smell.

The specimens of the fungus which I examined in Bermuda consisted of a fine mycelium, which ramified through all the superficial tissues of the onion-leaf. The mycelium was septate, consisting of numerous elongated cells with granular contents. The cells occasionally branched, and frequently gave off fertile hyphae. It was noticeable that the hyphae ramified *through the cells of the host and not between them*, in marked contrast to the *Peronospora*. The fertile hyphae always bored their way to the surface through the outer cell-wall of the epidermis, their apices apparently exerting some solvent action on the cellulose. I do not remember ever having seen the hyphae projecting through the mouth of the stomata, as Mr. Kingo Miyabe describes, though it was not uncommon to find these hyphae growing through the guard-cells.

The description of these hyphae given by Mr. Kingo Miyabe appears to me to be very accurate, but the spores borne at their ends consisted, in the species examined at Bermuda, of many more cells than those described in the paper above-mentioned. Twelve or more cells were not unfrequently seen in the larger spores, for they varied greatly in size; and from each of these, hyphae grew out, which, by their branching and interlacing, form the white fluff described above. These hyphae often have secondary spores at the ends of the branches as described by Mr. Kingo Miyabe from his water-cultures.

In an appendix to this paper Professor Farlow states that the investigation of which it treats was undertaken with a view of determining 'whether the *Macrosporium* was merely a fungus which had attacked plants previously suffering from *Peronospora*, as most botanists would suppose, or whether it might not of itself cause a disease of onions.'

The answer to this question is one of great importance to the inhabitants of Bermuda, for about four-fifths of their whole exports consist of onions. Professor Farlow is of opinion that 'the possibility that *Macrosporium* can grow in the tissues of living plants free from *Peronospora* seems to have been demonstrated.' Mr. Kingo Miyabe's experiments on this point do not, however, seem to me entirely conclusive. He says, 'A great number of young plants were started both from seeds and bulbs. The spores were sown on different parts of the leaves; and the pots were kept moist under bell-jars, with the exception of a few which were left uncovered. The greater part of the seedlings were greatly injured by nematoid worms, but those which survived did not show any sign of the attack. Out of the twelve bulbs, the culture on only two was successful. The spores, however, grew in both cases on the sheath of the leaves, and not on the active green portions.' Of these two specimens, one failed to produce perithecia, and in the other the perithecia were arrested when some of them were large enough to form paraphyses. In the experiments, although everything was in favour of the fungus establishing itself in the onion—even the attacks of the Nematodes would *weaken* the plant and render it a more easy victim—only two out of a great number of seedlings and plants grown from bulbs were infected, and these on the comparatively inert leaf-sheath. Again, the fungi which did establish themselves on these two plants either failed to produce perithecia, or else produced arrested ones. In this connection it should be remembered that a plant may be living whilst part of its tissue is dead, and is consequently a suitable nidus for saprophytes. If, however, we allow that these two instances afford sufficient ground for stating that *Macrosporium* can, under the most favourable conditions, grow on the tissues of living plants in a laboratory, it does not prove that, in a state of nature, it can produce a disease.

I have examined many hundred diseased onions in all stages of the attack, but I never saw one suffering from the black mildew (*Macrosporium*) which had not previously been attacked by the white (*Peronospora*); and I see no reason to believe that *Macrosporium parasiticum* is capable of causing a disease amongst onions.

I have unfortunately not been able to find in our libraries here the agricultural journals containing the papers quoted by Mr. Kingo Miyabe in reference to the parasitism of *Pleospora herbarum* which he has shown to be the ascosporous stage of *Macrosporium parasiticum*. I have, however, been able to refer to Professor Berlese's article on

Pleospora, Clathrospora, and *Pyrenophora*[1], in which he describes this form living parasitically upon *Sambucus nigra.*

The following quotation will show that Professor Berlese is also of opinion that this fungus does not cause any disease, but attacks only the most external parts and the dead tissue of the cortex:—'La *Pleospora herbarum* è un fungo saprofita, e che non determina alcuna malattia, e tutt' al più concorre a rendere più pronte e più efficace l'azione deleteria del morbo. Io lo riscontrai sui rami vivi di *Sambucus,* ma è probabile che esso intacchi soltanta le parti più esterne e di tessuto morto della corteccia.'

A. E. SHIPLEY, Cambridge.

ON THE MECHANISM OF THE STOMATA.—Until the publication of Leitgeb's important researches on this subject, it had been generally assumed, from the observations of Moldenhauer[2], Amici[3], and von Mohl[4], that the opening and closing of the stomata was a function of light; light inducing opening, darkness closing. The explanation offered by von Mohl of the action of light is briefly this: that, on account of the chlorophyll-corpuscles which they contain, there are formed in the guard-cells, under the influence of light, osmotically active organic substances; and that, under these circumstances, the guard-cells absorb water in such quantity as to induce a high degree of turgidity, and thus to enable them to overcome the compression exercised upon them by the adjacent epidermal cells. In darkness, these osmotically active organic substances are no longer formed; consequently the high degree of turgidity of the guard-cells can no longer be maintained, and the stomata close.

It was subsequently suggested by Sachs[5] that light may exercise a direct influence upon the molecular condition of the protoplasm of the guard-cells, of such a nature that, with increasing intensity of illumination, the protoplasm becomes more resistent to the escape of water from the cells; in a word, that the opening of the stomata in the light is the result of the stimulation of the irritable protoplasm (*Reizerscheinung*). This suggestion, however, simply results in a

[1] Nuovo Giornale Bot. Ital. vol. xx, 1888.

[2] Moldenhauer, Beiträge zur Anatomie der Pflanzen, 1812.

[3] Amici, Ann. d. sci. nat., t. 2, 1824.

[4] von Mohl, Botanische Zeitung, 1856, p. 717.

[5] von Sachs, Vorlesungen über Pflanzenphysiologie, 1ste Aufl., 1882, p. 300 (English edition, p. 250).

paradox. In all other cases, the influence of light upon irritable cells induces a diminution of turgidity. It is therefore improbable that the guard-cells of the stomata should react to light in the exceptional manner involved in Sachs' suggestion.

Leitgeb's[1] observations tend to prove that the guard-cells do not possess a specific irritability to the action of light. He finds that the main determining cause of the opening and closing of the stomata is the amount of water in the tissue, and the hygrometric state of the surrounding atmosphere. He gives up, in fact, the idea that the protoplasm of the guard-cells is irritable at all, and his views have since been accepted by Sachs[2].

It is not a little remarkable that Leitgeb should have abandoned the theory of the irritability of the guard-cells, when some of his own observations seem to indicate it so clearly. The reason for this oversight is apparently this, that Leitgeb confined his attention to the opening of the stomata, neglecting the closing.

It is, nevertheless, in the closing of the stomata that evidence in support of the irritability is to be sought; for in all cases of movement known among plants, the movement due to stimulation is associated with a diminution of turgidity.

The particular observations of Leitgeb which seem to indicate an irritability of the guard-cells in connexion with the closing of the stomata, are those which establish the fact that when a plant, or a part of a plant, is brought into a comparatively dry atmosphere, the stomata close. It had been previously observed by Amici and von Mohl that the stomata of withering leaves are closed, a fact which can, apparently, be easily explained on the assumption that, under these conditions, the guard-cells, like the other cells of the leaf, become flaccid. This explanation is, however, open to the criticism that, under these conditions, the epidermal cells, having become flaccid, would tend to drag the guard-cells apart, and so to open the stomata. Moreover, it is rendered untenable by the fact, recorded by Leitgeb, that it suffices to bring a plant from a damp to a dry room, to cause closure of the stomata; in other words, that the stomata close when there is no indication of general flaccidity of the leaf-tissues.

[1] Leitgeb, Beiträge zur Physiologie der Spaltöffnungsapparate, in Mitth. aus dem Bot. Inst. zu Graz, 1^es^ Heft, 1886.

[2] von Sachs, Vorlesungen, 2^te^ Aufl., 1887, p. 231.

It appears, further, from Leitgeb's observations, that the dryness of the atmosphere is not, in itself, sufficient to cause closure of the stomata, but that the amount of water present in, or supplied to, the leaves, is an important factor. The closing of the stomata seems to depend upon a certain relation between the dryness of the air, on the one hand, and the amount of water in the transpiring tissue, on the other.

The problem is one which demands further investigation for its complete solution, and I hope to be able to carry out some experiments in this direction. But I may venture even now to offer some suggestions in explanation of the mechanism of opening and closing.

In the face of Leitgeb's observations, there can be no doubt that the opening of the stomata is not due to stimulation, by light or any other agent, of the irritable protoplasm of the guard-cells. The process is a purely passive one, depending upon the formation of osmotically active organic substances in the chlorophyll-containing guard-cells when exposed to light. This view is supported by Leitgeb's account of the opening of the stomata, in which he describes the gradual disappearance of the granules in the protoplasm, and of the starch-granules in the chlorophyll-corpuscles, in the turgescent guard-cells of the opening stoma; and, further, by N. J. C. Müller's [1] observation that a rise of temperature promotes the opening of the stomata.

It may be objected that this theory does not account for the opening of the stomata of etiolated plants, or for that of normal plants in darkness. In reply to this objection it may be pointed out that, as Sachs [2] first demonstrated, the guard-cells of even etiolated plants always contain starch-granules, and that therefore they have the means of ensuring endosmosis and consequent turgidity.

The closing of the stoma is, on the contrary, an active process, determined by the stimulating influence of a certain relation between loss and supply of water, on the irritable protoplasm of the guard-cells.

I cannot more clearly state this view than by the following quotation from N. J. C. Müller: 'Die Oeffnungsstellung ist die normale Stellung des Apparates; die Schliessungsstellung ist die Reizstellung;' though the stimuli referred to by Müller are other than the one which I suggest. The theory of the function of the stomata which logically follows from this view is essentially the same as that originally pro-

[1] N. J. C. Müller, Pringsheim's Jahrb. f. wiss. Bot., VIII, 1872.
[2] von Sachs, Botanische Zeitung, 1862, and 1863, Beilage.

pounded by Sir Joseph Banks[1], that the stomata are regulators of transpiration, closing when the conditions are such as to promote excessive loss of water.

It is, of course, admitted that the state of the stoma may not in all cases entirely depend upon the turgidity or flaccidity of the guard-cells, but that it may be affected by the degree of turgidity of the adjacent epidermal cells when the anatomical relations are such as to permit it[2]. But it may be pointed out that this influence works practically in one direction only, that of ensuring the closing of the stomata. For instance, in the case of a plant, such as *Amaryllis*, in which these anatomical relations obtain, the effect of a high turgidity in the epidermal cells could only be to close the stomata even when the guard-cells are highly turgid and tend to separate. A low degree of turgidity in the epidermal cells of such a plant would be, in the first instance, necessarily accompanied by a low degree of turgidity in the guard-cells and closing of the stomata. It is probable that a fall in the turgidity of the epidermal cells sufficient to forcibly drag apart the guard-cells could only take place in the event of the complete drying-up and death of the tissues.

In conclusion I may point out that this view of the irritability of the guard-cells of the stomata is supported by the little that is known as to their reaction to other stimuli. Müller observed that induction-shocks cause the stomata to close; but not much weight can be attached to this, for it appears that these shocks caused the death of the guard-cells. More important is the observation of Baranetzky[3], that when a leafy branch is violently shaken, the transpiration is momentarily increased, but subsequently diminished, the diminution being ascribed to an induced flaccidity of the guard-cells and the consequent closure of the stomata.

S. H. VINES, Oxford.

[1] Sir Joseph Banks, An account of the cause of the disease in corn, König and Sims' Annals of Botany, II. 1806.

[2] See also Schaefer, Ueb. den Einfluss des Turgors der Epidermiszellen auf die Function des Spaltoeffnungsapparates, Diss. Inaug., Berlin, 1887.

[3] Baranetzky, Botanische Zeitung, 1872.

On the Anatomy and Histogeny of Strychnos.

BY

D. H. SCOTT, M.A., Ph.D., F.L.S.,

Assistant Professor in Botany, Normal School of Science and Royal School of Mines,

AND

GEORGE BREBNER.

With Plates XVIII and XIX.

THE dominant position which the Dicotyledons unquestionably hold among existing forms of vegetation is probably due in a greater degree to their method of secondary growth in stem and root, than to any other single character. The ability to increase indefinitely the amount of mechanical, conducting and storing tissues in the axial organs, in proportion to the increasing development of the foliage, has more or less generally existed in all the most successful classes of plants; but it is in the Dicotyledons that the highest differentiation of the secondary tissues is attained. The ascendancy of the Dicotyledons is most marked among those forms in which the duration of life renders a considerable secondary growth possible. The study of the modifications in the secondary formation of tissue in this class is therefore an important branch of biological inquiry. Though the process in its typical form is so well known, the recent work of Robert Hartig and others shows that there is still

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much to be learnt, even from the best investigated cases. The state of our knowledge regarding those very numerous modes of secondary growth which are usually classed as 'anomalous' is much less satisfactory. Here as elsewhere the rule holds good that structure cannot be understood without development, and we still know but little of the development in a large proportion of these cases. It is the object of the present paper to clear up, as regards one anomalous genus, some of the points which previous investigations have left obscure.

Literature of the Subject.

The original literature relating to the anatomy of *Strychnos* is very meagre, and so far as we are aware, is the work of three investigators only. The peculiar structure of the stem appears to have been first noticed by Fritz Müller[1]. He found that the wood is traversed by a number of isolated strands of soft tissue, but he was not in a position to make any microscopic observations, and so the exact nature of this tissue could not be ascertained. The first to make any detailed investigation of the subject was de Bary[2], and his account is still the one generally accepted. His work is so familiar to English readers that it is unnecessary to do more than give the briefest possible summary. De Bary found that in the stem there is at first a normal ring of bicollateral leaf-trace bundles. The external primary phloëm consists of small groups of cells, among which sieve-tubes could not be demonstrated with certainty. The cambium appears in the normal position, but forms no sieve-tubes in the secondary bast. Its activity is for a time almost entirely centrifugal, producing secondary wood only. At a later stage considerable additions are made to the external bast, but only in the form of phloëm parenchyma, and, in some species, of short-celled sclerenchyma. The secondary sieve-tubes are situated

[1] Über das Holz einiger um Desterro wachsenden Kletterpflanzen, in Bot. Zeitung, 1866, p. 68, Fig. 10.

[2] Vergleichende Anatomie d. Vegetationsorgane, 1877. Eng. ed. 1884, pp. 578–580.

in the wood. They form, together with thin-walled parenchyma, isolated strands surrounded on all sides by the tissues of the xylem. According to de Bary 'suitable developmental stages easily show that these phloëm-strands in the wood are given off by the cambial zone towards the inside[1].' It should be noted that de Bary had no fresh material of the stem more than 1 mm. in thickness. All his observations relating to the anomalous secondary growth were made on dry material. His Fig. 229, the only one given, is a diagrammatic, slightly magnified transverse section, and throws no real light on the development. A similar structure is described in the malpighiaceous genus *Dicella*, which was also one of the plants observed by Fritz Müller.

In another passage[2] de Bary draws a comparison between the structure of *Strychnos* and that of certain Chenopodiaceae, and formulates a general rule, applicable to all such cases, that all secondary tissue formed centrifugally inside the cambium is to be regarded as wood, while all that is formed centripetally on its outer side belongs to the bast. On this principle the secondary phloëm-strands of *Strychnos* come under the category of wood. With one exception, to be mentioned immediately, all later writers on the subject seem to have simply adopted de Bary's statements as to this genus[3]. We shall see later on that the anatomical peculiarity consisting in the presence of phloëm groups imbedded in the xylem is now known to occur in many genera besides the two mentioned by Fritz Müller and de Bary.

Hérail's *Recherches sur l'anatomie comparée de la tige des Dicotylédones*[4] contain a valuable series of observations on the development of anomalous stems, and *Strychnos* is among the genera investigated. His account of the development is much the most satisfactory which we possess, His chief results are as follows: he finds, in agreement with de Bary,

[1] l. c. p. 579. [2] l. c. p. 591.

[3] See for example Van Tieghem, Traité de Botanique, p. 796; and Solereder, Über den systematischen Werth d. Holzstructur b. d. Dicotyledonen, 1885, p. 178.

[4] Annales des Sciences Naturelles, sér. vii, T. ii, 1885.

that the production of external secondary bast is at first very slight. When the stem is two years old the outer boundary of the wood becomes uneven, and its depressions are filled by little groups of phloëm, which subsequently become the 'phloëm-islands[1].' The cambium remains in contact with the wood during their development, and hence the phloëm-islands must be produced on its exterior side. The intercepted portions of the wood are reunited by means of divisions in the cells of the pericycle lying outside the newly formed phloëm group, and thus the latter becomes imbedded. Hérail compares this process with that in *Bignonia*, in which the phloëm-plates are also formed by increased centripetal and diminished centrifugal activity of the cambium at certain points, though in *Bignonia* the phloëm does not become enclosed in the wood. The fact that regular radial rows of cells, continuous with those of the wood, can only be traced in the *inner* part of the phloëm-islands, is used by Hérail as an argument in favour of their centripetal development. He concludes by pointing out that *Strychnos* conforms to the 'general law' that a cambium only forms one kind of tissue, wood or bast, on each of its faces. He gives two figures, one of which (Fig. 24) accurately represents a developing phloëm-island, showing clearly the continuity of the radial series of cells inwards, but not outwards. The other figure will have to be referred to again later on. The main point is, that Hérail's account directly contradicts that of de Bary. According to the former the phloëm-islands are formed centripetally, and thus belong, like other phloëm, to the bast tissues, while, as we have seen, de Bary believed that they are formed centrifugally, and are thus a constituent of the wood.

We will now proceed to describe our own observations, deferring all comparative consideration of parallel cases to the end of the paper. It may be mentioned that the essential part of our work, in so far as it relates to the development of

[1] This name is so appropriate for the isolated phloëm-groups imbedded in the xylem, as they appear in transverse sections, that it will be adopted throughout this paper.

the phloëm-islands, had already been done before we became acquainted with Hérail's paper, so that our points of agreement with him afford an independent confirmation of his statements.

General Structure of Stem.

Before tracing the development in detail, it will be useful to give a short description of the structure of a well-developed stem. If a transverse section of an internode of *Strychnos nux vomica*, L., not less than 5 mm. in diameter [1], be examined, the following structure is observed. On the outside is an external periderm, consisting of several layers of cork, with scanty phelloderm. Within this is the parenchymatous cortex, of no great thickness, and then a dense two-layered ring of very sclerotic cells. This immediately surrounds the radially arranged bast-parenchyma. In its outer region the small groups of primary phloëm may still be recognized here and there. Next comes the cambium, and within this the broad zone of wood, occupying much the greater part of the whole area. Scattered about in the wood, and arranged irregularly in three or four concentric rings, we find the phloëm-islands, roundish groups of soft bast separated from one another by broad tracts of the continuous mass of wood. At the inner boundary of the wood lies the ring of medullary phloëm-groups, intruding into the pith. They are usually about twelve in number, and are of almost the same size as the phloëm-islands in the wood. The pith itself is rather thick-walled, and in our specimens is of uniform structure throughout, containing abundant starch. One very conspicuous point is, that all the medullary phloëm-groups, and all the more deeply-seated islands show great masses of crushed and obliterated tissue, and it is at once seen that in the phloëm-islands of the wood the obliterated tissue invariably lies on the outer side, while in the medullary groups it is as constantly

[1] The stem in question was at least five years old, probably more. We were not able, in hot-house grown plants, to distinguish the annual rings with certainty beyond the second year.

situated on their inner side, towards the pith (compare Figs. 5 and 11). Conversely, the living, functional tissue always occupies the inner part of the phloëm-islands, and the outer part of the medullary groups. This fact of the obliteration of effete portions of the phloëm in both regions does not appear to have been noticed by any previous observers, probably because their material was either too young, or if older was herbarium material, in which the soft tissue is all so disorganized that it is impossible to distinguish between its active and its obliterated portions. The facts just mentioned afford a most valuable clue to the direction of development in both cases. Another point which is easily observed is, that in the phloëm-islands the radial rows of cells can always be readily traced inwards into the wood, while no such continuity exists in the opposite direction. It was the observation of these two classes of facts which first led us to question the accuracy of de Bary's account of the development, and to infer that the medullary phloëm-groups are developed centrifugally, but those in the xylem centripetally [1].

Development of the Stem.

The earliest stage of development observed was in *S. spinosa*, Harv., in a stem about 0·6 mm. in thickness. Within the epidermis is a cortex consisting of about three layers of short parenchymatous cells. Next to this comes the pericycle, which is three to four layers thick; the outer layers are formed of rather elongated parenchyma (not readily distinguishable from the external cortex in transverse section), and the innermost layer consists of multinucleate prosenchymatous elements, often radially elongated as seen in transverse section. In the ring of leaf-trace bundles the protoxylem elements already have spirally thickened walls. The xylem

[1] As confusion has occasionally arisen from the use of these words, it may be well to state expressly that development is said to be *centrifugal* when each new element cut off from the cambium lies further from the centre of the axis than the next older element, while the converse order of development is termed *centripetal*.

is arranged in regular radial rows (only two elements in each row usually having thickened walls). This points to the occurrence of regular cambial divisions even at this early stage. The interfascicular tissue also shows a radial, though less regular arrangement of its cells. The small external phloëm-groups, evidently produced by cell-divisions in all directions equally, are in immediate contact with the pericycle. There are usually two of these groups to each bundle, but they also occur opposite the interfascicular tissue. The internal (medullary) phloëm groups are much larger than the external ones, though only about half as numerous. It may be estimated that they already contain collectively twice as many cells as there are in the external phloëm. The cells of the medullary phloëm show some signs of a radial arrangement (cf. Fig. 1). The pith is thin-walled throughout. It is clear then that the medullary phloëm is a primary formation developed simultaneously with the protoxylem and the external phloëm, and that thus the bundles are bicollateral from the first. The internal phloëm accompanies the bundles on their exit into the leaf. The transverse section of a petiole shows five bundles, arranged in a curved row, concave towards the upper surface. All these bundles are bicollateral, the superior phloëm-groups being often more developed than the inferior. In the main bundles of the lamina, the bicollateral structure is still preserved, both phloëm-groups having about the same extent; the smaller bundles, however, are of the normal collateral type with inferior phloëm only. The medullary phloëm of *Strychnos* thus possesses the characters which Petersen [1] and Weiss [2] have found to be general in other bicollateral bundles. It forms an integral part of the leaf-trace bundle to which it belongs.

De Bary did not decide whether the normal external

[1] Ueber das Auftreten bicollateraler Gefässbündel, u. s. w., in Engler's Jahrbuch für Systematik, Bd. iii, 1882, p. 391.

[2] Markständiges Gefässbündelsystem und Blattspuren, in Bot. Centralblatt, Bd. xv, 1883, pp. 396, 401.

phloëm of *Strychnos* contains sieve-tubes or not. This question can be best investigated at a stage slightly later than that just described. In transverse sections the horizontal sieve-plates can be recognized as dotted areas, while the longitudinal section shows that these plates are perforated. Normal companion cells accompany the sieve-tubes. The latter, however, sometimes contain nuclei, which in most sieve-tubes disappear at an earlier stage, and this fact may point to the rudimentary character of the normal phloëm here (see Figs. 2 and 3).

Later stages of development from the same plant show that the cambial divisions go on in those cells which are in immediate contact with the external phloëm. Even when the wood has increased to a thickness of sixteen to eighteen cells, no considerable addition has taken place on the outside of the cambium. The outer layers of the pericycle undergo sclerosis, while its prosenchyma first becomes thick-walled, and is then obliterated. The structure of the pericycle is a character which differs very much among the different species of the genus. Other material, probably of the same species, but from a different source, showed the formation of a hypodermal phellogen producing cork centripetally, and abundant phelloderm centrifugally. The phelloderm contains many sclerotic cells. The normal cambium increases its activity, and produces large quantities of bast parenchyma and short-celled sclerenchyma. At this stage the stem has no less than four distinct consecutive zones of mechanical tissue in its cortical region. Towards the exterior are the sclerotic cells of the phelloderm, then those of the pericycle, next the fibres of the pericycle (soon becoming obliterated), and lastly the secondary sclerenchyma of the bast. Cambial increase of the medullary phloëm groups soon begins, by means of divisions in the cells situated towards the protoxylem, and a certain amount of obliteration on the inner side of the group is the result.

Petersen[1] found that in a large proportion of the plants

[1] l. c. p. 395.

with medullary phloëm the periderm is internal, so that the normal phloëm comes to lie dangerously near the surface. This is not the case in *Strychnos*. In the species examined the periderm was always external (hypodermal in some, epidermal in others, e.g. *S. Grayi*, Griseb.), and though the primary cortex is often thin the external phloëm is very well protected by sclerotic tissue, and is exposed to no greater risks than in most normal plants.

It may be noticed that in the older specimens referred to *S. spinosa*, groups of very beautiful stone-sclerenchyma occur in the pith.

More advanced stages of development were chiefly observed in *S. nux vomica*, L. The anatomy of the stem differs in some points from that of *S. spinosa*. The primary cortex is thicker, consisting of about seven layers of cells. The pericycle is limited externally by a single layer of very long fibres with thick cellulose walls. These elements are multinucleate when young. Within the fibres there are one or two layers of parenchyma, and then comes a sclerotic ring, usually two layers thick, of very thick-walled lignified cells, which are parenchymatous in form, but of very variable length[1]. The minute groups of external phloëm either abut directly on the sclerotic ring, or in some cases are separated from it by a single parenchymatous cell. These phloëm-groups are even more rudimentary than in *S. spinosa*. The centripetal activity of the cambium is for a time very slight. When the xylem is from ten to fourteen cells in thickness, its outer margin is often separated from the sclerotic ring by three cells only, including the cambial layer. The wood itself shows no special peculiarities. Besides the spiral vessels of the primary xylem, it consists of vessels with bordered pits, very abundant and thick-walled libriform fibres, woody parenchyma, and medullary rays one to three cells in thickness. The groups of medullary phloëm are of large size. At the stage we are describing the larger groups are about fourteen cells and the smallest about

[1] The pericycle of this species was described by Morot, Recherches sur le péricycle, in Ann. des Sci. Nat. sér. 6, T. xx, 1885, p. 264.

nine cells in radial thickness. They are separated from the inner margin of the wood by two or three layers of somewhat flattened parenchyma resembling that of the pith. The earlier stages, however, prove that these cells form part of the original procambial strand, and so do not properly belong to the pith[1]. Cambial divisions of the cells at the outer edge of these phloëm-groups go on more actively than in *S. spinosa*, and the increase of their tissue soon leads to the obliteration of the elements lying towards the pith. It is not necessarily the case that this obliteration advances regularly from within outwards. Often a row of obliterated cells is seen at the extreme inner margin; next we find a row of still normal cells, and then another obliterated layer. The older sieve-tubes are evidently the first elements to yield to obliteration, while the turgid parenchymatous cells offer a longer resistance. As regards the primary structure of the medullary phloëm, it consists of sieve-tubes with somewhat inclined transverse sieve-plates, companion cells, and phloëm parenchyma, the cells of which are about eight diameters in length. The pith itself is of uniform structure throughout, consisting of parenchymatous cells of variable length, full of starch, with thickened, pitted, and somewhat lignified walls. It forms an unyielding matrix in which the phloëm-groups have no room to expand (see Fig. 4).

We will complete the history of the medullary phloëm before going on to the other tissues of the stem. The centrifugal activity of the special cambium[2] goes on until a large part of each group (sometimes its entire inner half) becomes obliterated, forming a stratified mass of 'Hornbast,' with no cavities left in it beyond mere cracks. The cambial cells can still be recognized in Fig. 5, but their activity has evidently slackened. There is no centripetal formation of tissue worth mentioning;

[1] Cf. Petersen, l. c. p. 391.

[2] Vesque calls meristem in this position 'false cambium,' chiefly because its productiveness is only unilateral. This is not a constant character, and 'special' or 'local' cambium is a less objectionable term. Cf. Vesque, Anatomie comparée de l'écorce, in Ann. des Sci. Nat. sér. 6, T. ii, 1875, p. 138.

only one cell is usually cut off on the side towards the wood. The secondary sieve-tubes formed by the local cambium have inclined walls, each of which sometimes bears three sieve-plates. The cambial cells are perhaps best studied in a radial section, in which they are easily recognized by their abundant protoplasm and conspicuous nuclei. The sieve-tubes appear to lose their contents before obliteration, and sometimes show a little callus on their plates.

In *S. nux vomica*, as in *S. spinosa*, a hypodermal periderm is formed, but in the former species there is little phelloderm. The fibres of the pericycle become obliterated, while the sclerotic cells increase in number, probably by sclerosis of some of the outer cells of the bast parenchyma. The latter eventually receives considerable additions from the cambium, and at the stage now to be considered is about six cells in radial thickness. The external groups of soft-bast become almost wholly obliterated by the pressure of the newly formed cells.

Development and Structure of the Phloëm-Islands.

The formation of the phloëm-islands begins late in the second year of growth, at least this was certainly the case in those stems where the annual rings could be distinguished with certainty. At this period the wood is from thirty-five to forty-five cells in radial thickness. As regards the position of the phloëm-islands relative to the primary bundles we have found no general law. The position is best determined with reference to the medullary phloëm-groups which always lie immediately inside the primary xylem-strands. Sometimes the first formed phloëm-islands lie opposite every alternate medullary group, and later on a second ring of islands is formed alternating with the first, so that every medullary group now has a phloëm-island corresponding to it. But this does not always hold good, for sometimes even the first formed islands lie in

the interfascicular tissue, and not opposite a primary bundle at all, and after the first two rings are formed all regularity of arrangement ceases.

We will now trace the development of a phloëm-island (see Fig. 6). The first sign of its appearance is the increased activity of cell-division in a portion of the normal cambium. Otherwise the cambial divisions go on very slowly (at least in hot-house specimens), and wherever a number of fresh tangential cell-walls are apparent we may infer that an island is about to be formed. The cambium is at all stages of the development in contact with lignified cells on its inner side, so the formation of centrifugal phloëm, as described by de Bary, is out of the question (Figs. 6, 7, 8, 9, and 10). The development of the island is due to increased centripetal activity. There is not at first any corresponding diminution in the wood-forming productiveness of this portion of the cambium, and so the outer margin of the secondary wood may remain for a time unbroken. Thus the depressions ('anfractuosités') in the wood on which Hérail[1] lays stress are not a necessary concomitant of the origination of the phloëm-islands. They are in fact very misleading as a clue to the earliest stages, for irregularities in the outline of the wood are frequent, independently of the islands, and we have already seen that the converse is also the case. After a careful comparison of Hérail's Fig. 23 with our own preparations we cannot feel convinced that this figure really represents the origin of a phloëm-island at all. The groups marked *l* are certainly *primary* phloëm, which may or may not happen to lie opposite the place of development of an island, and which in any case take no part in its formation. The phloëm of the islands is, as we shall see, the direct product of cambial divisions, and bears no resemblance at any stage to the small-celled groups shown in Hérail's figure. His statement therefore that these groups 'become' the phloëm-islands cannot be accepted, though in other respects his account agrees with our observations.

As additional phloëm-elements are formed on the outside of

[1] l. c. p. 258.

the centripetally active cambium, the growing tissue has to find room among the pre-existing bast-parenchyma, which consequently becomes locally compressed. At this stage the transverse section of the developing island has the form of a segment of a circle (the cambium forming the chord), which projects into, and displaces the bast-parenchyma. Among the crushed elements bordering the new tissue one of the primary phloëm-groups may occur, but this is not constantly the case. The cells cut off by the cambium rapidly pass over into permanent tissue. Each sieve-tube is formed directly from a cambial cell, the only divisions which it undergoes being those by which its companion cells are formed (see Figs. 6 and 8).

The space required by the developing phloëm-island is however only partly provided by displacement of the external tissue. The cambium forming the island soon ceases, or nearly ceases to produce wood, and its activity in phloëm-formation now just balances the activity of the normally wood-forming cambium on either side. Hence the new phloëm comes to be flanked on the right and left by newly formed secondary xylem, and thus lies in a depression of the woody mass (see Fig. 7). That this process must be accompanied by 'sliding growth' between the phloëm and the adjacent wood is evident here, as it is in the case of the phloëm-plates of *Bignonia*, with which the islands have already been compared by Hérail [1]. Hence we find that the parenchymatous cells lying on the flanks of the island become stretched in the radial direction. The unequal formation of xylem and phloëm further results in the fact that the phloëm-forming portion of the cambium becomes detached from the normal ring, and remains nearer the centre of the stem. Thus the main zone of cambium has now suffered an interruption of its continuity. But this interruption is only temporary. The process just described goes on until the phloëm-island has

[1] For a very full account of the development of the phloëm-plates in *Bignonia*, see Hovelacque, Recherches sur l'appareil végétatif des Bignoniacées, etc., 1888, pp. 60–69.

attained its definitive form. Then the activity of the phloëm-forming cambium slackens, though it does not cease, and so the margin of the wood comes up flush with the outer margin of the phloëm-island. And now those cells of the external bast-parenchyma which have escaped obliteration begin to divide, starting on either side with the cells adjacent to the normal cambial zone. The divisions advance from both sides until the cambium becomes continuous around the outer border of the island, and the normal ring is once more completed (Fig. 9).

The exact position of the cells which divide, in order to complete the cambial zone, varies. They may either lie immediately outside the external sieve-tubes of the island, separated from them only by a layer of obliterated cells; or they may lie further towards the exterior, leaving one or two rows of living parenchyma between the new cambium and the outer border of the actual phloëm. The cambial arc by which the normal ring is completed requires a name. We propose in this, and in all similar cases, to term it *complementary* cambium. A word must be said as to the nature of the cells by the divisions of which it is formed. Hérail speaks of them as belonging to the pericycle. This may be true in some species, in which the pericycle remains largely parenchymatous, but in *S. nux vomica* the inner cells of the pericycle become sclerotic, and the cells which undergo division, as shown by their position and regular radial arrangement, both in transverse and longitudinal sections, are clearly of secondary origin, and come under the head of bast-parenchyma.

The complementary cambium now assumes its normal function as part of the general ring. It begins to form wood, outside the new phloëm, starting on either side (Fig. 10). The wood thus formed becomes continuous, and the phloëm-island is now completely surrounded, and deserves its name.

The cambium on the inner side of the island does not however cease its activity. It goes on for a long time producing new and active phloëm as the old becomes past work, and the

new elements can only find room by the crushing and obliteration of the old. The nearer the island lies to the centre of the stem (i. e. the older it is) the greater of course is the amount of obliteration. In the oldest observed, the mass of crushed elements, which as we have seen always lies on the outer side of the island, may occupy almost half its area (see Fig. 11). Towards the inner side, on the other hand, a distinct cambial layer, with thin tangential cell-walls, is always found. As we have already seen, it is a constant rule that the radial arrangement of the phloëm-elements is most regular in the inner part of the island, and that the radial series can be traced continuously inwards through the cambium into the wood. Towards the outside the radial rows, even when not wholly erased by obliteration, can seldom be traced at all, and never with any regularity. That any signs of radial continuity can ever be seen on the outside is due to the fact that the complementary cambium (in this species at any rate) arises by the division of cells which were themselves of cambial origin.

Some account must be given of the position of the phloëm-islands in the wood; and first, as regards their relation to the medullary rays. A small island often occupies the space between two rays. In other (rarer) cases, a medullary ray can be clearly traced straight through the island. In one case a large ray, three cells thick, was observed to pass through the middle of an island, its cells being thin-walled in this part of its course. At the outer margin of the phloëm the cells of the ray are not obviously distinct from the parenchyma so often found at the outside of an island, but in the external wood the ray goes on again as before. These facts are explained by the development. The complementary cambium has simply formed new ray-cells which approximately fit on to those which the normal cambium had begun to form before its dislocation. Not uncommonly however a broad secondary ray starts from the outer margin of a phloëm-island. In other cases a small ray can be traced to the inner margin of an island and through the cambial layer into its tissue, but it does not reappear on the outside. The explanation of all

these various cases is obvious in the light of the developmental facts.

It is a nearly constant rule that the island is bounded on its outer side by woody parenchyma; its inner boundary is usually, but less constantly, formed by woody fibres. The xylem-elements abutting laterally on the islands may be ray-cells, woody parenchyma, or fibres. We have never found vessels in contact with the islands. On the outer side and on the two flanks the contrast between the thick-walled xylem and the soft phloëm is quite sharp. On the inner side, however, a layer or two of thin-walled cells are generally found between the woody fibres and the actual cambium, and among these cells developing xylem-elements may sometimes be observed. This proves that the phloëm-forming cambium has not wholly lost its capacity for centrifugal formation of wood.

The sectional form of a phloëm-island is circular, or more often somewhat elliptical, with the major axis directed tangentially to the surface of the stem. Its cambial-layer is thus curved, with its convexity towards the centre of the stem. This is due to the fact that during the formation of the island the retardation of the wood-forming activity of its cambium begins at the middle point of the layer.

As regards the minute structure of the phloëm-islands we have nothing to add to de Bary's account, except that the elongated cambial cells on the inner side are very conspicuous in radial section (Fig. 8). The phloëm is made up of parenchyma, sieve-tubes, and companion cells. The first-formed sieve-tubes of the island have approximately transverse sieve-plates (Fig. 8), but those which are developed later on have inclined terminal walls, sometimes bearing three sieve-plates each. The direction of inclination of these walls is variable, as would be expected from the curved course of the cambial layer, and from the great crowding of the cells. Anastomosis of the phloëm-strands in the internodes is certainly rare, if it ever occurs, but they unite with one another at the nodes.

Structure of the Root.

We are not acquainted with any previous observations on the *root* of this genus. We were not able to obtain material sufficiently advanced to decide the most interesting question, namely that as to the existence of phloëm-islands in the root. The oldest roots at our disposal had a xylem ring about eighteen cells in radial thickness, whereas in the stem the formation of phloëm-islands does not begin until about double this amount has been formed. Hence no negative conclusion can be drawn. We were able, however, to prove the existence of medullary phloëm in the root of *S. spinosa* (the only species examined), and as this appears to be an uncommon structure among Dicotyledons, it will be desirable to give some account of the anatomy of the roots of this plant.

The roots examined were from two sources, the Royal Gardens at Kew, and the garden of the Society of Apothecaries at Chelsea. The former plant is certainly *S. spinosa*, and the latter in all probability belongs to the same species. The differences in structure between the roots of the two specimens may well be due simply to differences of age. The largest roots examined were about 4 mm. in diameter. They are of polyarch structure, ten being a common number for the xylem or phloëm-groups. The cortex is wide, and persists for a long time. The hypodermal layer is cuticularized, and forms a well-marked exodermis. The subjacent cells often divide to form an external periderm. This is, however, only a temporary structure, for the pericycle ultimately gives rise to an internal periderm of great regularity. In the main roots the pith is relatively very large, the xylem for a long time forming only a relatively narrow ring. The formation of secondary phloëm is most active opposite the primary phloëm-groups, so that the latter become pushed out into the pericycle, causing local compression of tissue. The appearance of these prominent masses of phloëm is quite like that of the phloëm-islands of the stem at an early stage of development, but we have no evidence to show that the phloëm-groups of the root ever become enclosed in the wood.

Small groups of medullary phloëm lie just within some, but not all, of the primary xylem-groups. The cells between the medullary phloëm and the xylem form a distinct cambium (Fig. 12). The development of these phloëm-groups is very unequal. In the same transverse section some are found with fully formed sieve-tubes, while others are only indicated by a few cambial divisions in the outer cells of the pith. It appears then that the medullary phloëm in the root is of relatively late development. Similar structures are found in all the roots which have any pith. In the smallest lateral branches the xylem reaches to the centre, and here, of course, there is no medullary phloëm.

In some roots of the specimen undoubtedly belonging to *S. spinosa* the outer zone of the pith is sclerotic, so that the central parenchymatous portion is of relatively small extent. In such roots there is usually a single excentrically situated medullary phloëm-group. This may be separated by as many as three parenchymatous layers from the nearest sclerotic tissue. Here also a layer of cambium is present on the side towards the xylem. Longitudinal sections show that the medullary phloëm-groups of the root contain typical sieve-tubes and companion cells, the older sieve-tubes having their plates obliterated by callus.

Summary of Results.

Before going on to compare the phenomena of development in Strychnos with those in some other Dicotyledons, we will shortly recapitulate the results of our observations:—

1. The *external phloëm*, though but little developed, contains sieve-tubes and companion cells of normal structure, with the exception that nuclei are found in the mature sieve-tubes. The latter fact is perhaps an indication of their rudimentary character.
2. (*a*) The *medullary phloëm-groups*, as shown by their development and by their course, form an integral part of

the leaf-trace bundles, which are therefore from the first of bicollateral structure.

(*b*) These medullary groups grow by means of a special cambium lying on the outer side of each group. The formation of additional elements by the cambium results in the progressive obliteration of the older and effete portions of the phloëm on the side towards the pith.

3. (*a*) The *phloëm-islands*, or interxylary phloëm-strands, are formed centripetally by certain portions of the normal cambium. They become sunk into the wood owing to the relative retardation of the development of secondary xylem on their inner side. The wood ultimately closes round them in consequence of the formation of a complementary cambium, which arises from the division of cells of the external bast-parenchyma, and thus again completes the cambial ring.

(*b*) The phloëm-islands continue to grow, after they are enclosed in the wood, by means of the cambial layer on their inner side. This growth is opposite in direction to that of the medullary groups, and results in the obliteration of the older tissues occupying the outer part of the island.

4. The roots, in so far as they have a pith, possess medullary phloëm-groups, similar to, but smaller than, those of the stem, and increased, like the latter, by means of a centrifugally active local cambium.

Comparative Considerations.

In possessing bicollateral bundles *Strychnos* agrees with a large part of the Loganiaceae [1], and with many other natural orders of the most diverse relationships, among which the Myrtaceae, Onagraceae, Lythraceae, Cucurbitaceae, Melastomaceae, Solanaceae, Asclepiadeae, Apocyneae, Cichoriaceae, and Campanulaceae may be mentioned. This is not the place to discuss the systematic importance of this character, a

[1] See Solereder, l. c. pp. 28 and 176.

question which has been sufficiently dealt with by Petersen and Solereder. In several of these cases the normal external phloëm is much reduced, but this peculiarity is more generally characteristic of plants with phloëm-islands in the wood. In *Strychnos*, which is so abundantly provided with both medullary and interxylary phloëm, it can excite no surprise that the external phloëm should remain in a comparatively rudimentary state. The presence of a centrifugal cambium between the xylem and the internal phloëm of bicollateral bundles has already been often recognized. Vesque[1] found it in various Solanaceae, Asclepiadeae, and Apocyneae, and Petersen further showed that it occurs among the Myrtaceae, Lythraceae, Cichoriaceae and Campanulaceae[2]. He even states that in *Tragopogon* and *Lactuca* this cambium forms a little centripetal wood. The internal cambium of Strychnos, especially of *S. nux vomica*, appears to be exceptionally active in phloëm-formation, so much so that a comparison with *Tecoma* at first suggested itself. There is, however, no centripetal wood in *Strychnos*, and the medullary structures in *Tecoma* must certainly be regarded as constituting a distinct system of bundles, whether cauline as Hérail[3] and Hovelacque[4] believe, or common, as held by Weiss[5], and not as forming part of the bundles of the normal ring. However, the distinction is not really so sharp as it appears. Transitional cases between internal phloëm and distinct medullary bundles occur in the Melastomaceae, Solanaceae, Cichoriaceae, Campanulaceae[6], and other families.

As regards the presence of phloëm-islands in the wood, they are now known, chiefly owing to Solereder's work on herbarium material, to occur in no less than twenty-four genera, belonging to ten different natural orders; whereas when de Bary published his 'Vergleichende Anatomie' they were only known in the two genera *Strychnos* and *Dicella*. We will not enumerate all the genera, but will only mention the orders

[1] l. c. p. 146. [2] l. c. pp. 363 (Pl. IV, Fig 4), 370, 386, and 391.
[3] l. c. p. 282. [4] l. c. pp. 12, and 146–179. [5] l. c. pp. 396, etc.
[6] Cf. Petersen, l. c. pp. 371, 382, 386, 391; also Weiss, l. c. p. 396.

to which they belong. They are: Vochysiaceae, Malpighiaceae, Olacineae, Combretaceae, Melastomaceae, Salvadoraceae, Loganiaceae, Gentianeae, Acanthaceae, and Thymelaeaceae. Thus every sub-class of Dicotyledons is represented. To this list, as we shall presently see, the Onagraceae, Solanaceae, and Goodeniaceae should probably be added, while similar, though not identical structures are also found in the roots of Cruciferae and of Cucurbitaceae. But though the examples are so numerous, only a small minority of the plants in question have been investigated any further than was necessary to establish the bare existence of the anomalous structure. Solereder, who was the first to find interxylary phloëm in sixteen genera, worked entirely on herbarium material,—a fact which he regards as advantageous, on account of the authentic naming of the specimens investigated [1]. But accuracy of specific determination, desirable as it is, is no compensation for inexactness in the anatomical results. The examination of histological structure in dry material alone, may afford a useful clue to the empirical identification of species, but is seldom of any use when developmental questions are involved. Solereder's work is of value from the wide field it covers, and is highly suggestive of further research, but his statements as to development rest on no satisfactory basis. He defines interxylary phloëm-groups as 'those islands of soft bast in the wood, which are locally produced on the inner side by a normal cambium belonging to a normal circle of bundles [2].' This statement contains an unwarranted generalization. In the few cases in which the development has been traced, phloëm-islands are in some formed on the inner side, in others on the outer side of the cambium. We will shortly describe the best investigated instances of each.

Among the Vochysiaceae the phloëm-islands of *Erisma* have been observed and figured by Wille [3], who says that they are formed on the inside of the cambium. His figures,

[1] l. c. p. 7. [2] l. c. p. 32.

[3] Om Stammens og Bladenes Bygning hos Vochysiaceerne, Oversigt K. Dansk. Vidensk. Selskabs Forhandl. 1882–3. French résumé, p. 14.

however, are quite indecisive, and he admits himself that he could not obtain much information from the dry material he examined [1].

De Bary's investigation of the malpighiaceous *Dicella* [2] was also made on dry material. He comes to the same conclusion here as in *Strychnos*, but a re-investigation is obviously required.

Passing over several groups mentioned by Solereder, but of which we have no detailed knowledge as regards the point in question, we come to Salvadoraceae, an order not so very remote from the Loganiaceae. The phloëm-islands of *Salvadora* have been thoroughly worked out by Kolderup-Rosenvinge [3], and we have been able to confirm his statements. In this very interesting plant, which in habit resembles a fruticose *Strychnos*, the phloëm-islands are even more numerous than in that genus, and occur not only in the stem, but in the root and in the petiole of the leaf. The primary bundles, however, are not bicollateral. In the stem the islands resemble those of *Strychnos*, but contain rather more parenchyma. There is no doubt that they are formed centrifugally on the inner side of the normal cambium, and thus form morphologically a part of the wood. After an island is developed the same cambium resumes xylem-formation outside it, and so the phloëm becomes imbedded. In fact, the process which de Bary erroneously supposed to occur in *Strychnos*, actually takes place in *Salvadora*. After the phloëm is imbedded irregular cambial divisions go on, both towards the outer side of the island and elsewhere, and a certain amount of obliteration takes place towards the centre of the group. The external phloëm here is well developed.

In the root the structure is different. Here the islands consist chiefly of parenchyma. They are of large extent, and are often irregularly confluent with one another, as seen in transverse section. It appeared to us that the formation of the

[1] l. c. p. 187. [2] l. c. p. 580.

[3] Anatomisk Ondersoegelse af Vegetationsorganerne hos *Salvadora*, in Oversigt K. Dansk. Selskabs, 1880–81.

small phloëm-groups which are found in the parenchymatous islands is a secondary, or rather a tertiary process, like that of the interxylary bundles in the fleshy roots of Cruciferae, described by Weiss [1]. That is to say, certain of the secondary parenchymatous cells divide up to form a group of sieve-tubes and companion cells, which then increase in number by means of a special cambium surrounding the group on all sides. This, however, does not alter the main fact; the interxylary phloëm of the root, as well as of the stem, is developed, whether directly or indirectly, on the inner side of the normal cambium [2]. The accuracy of Kolderup-Rosenvinge's figures renders any illustrations of our own unnecessary.

As regards the Loganiaceae, we need only mention that Solereder found phloëm-islands in two additional genera, *Norrisia* and *Antonia*.

In *Chironia*, one of the Gentianeae, Vesque [3] found numerous small interxylary phloëm-islands. From his description and figures it is most probable, though not quite certain, that they are formed on the inner side of the cambium.

In *Thunbergia* and in *Hexacentris* (perhaps a sub-genus of the former) among the Acanthaceae, Vesque [4] found alternating tangential bands of phloëm and xylem, the origin of which was subsequently more fully investigated by Hérail [5]. He finds that this abnormality depends on the unequal activity of the cambium. Opposite the primary xylem-bundles the cambium forms abundant wood containing vessels, while between them it forms a smaller amount of wood destitute of vessels, but is so much the more active in the centripetal formation of phloëm. Hence the cambium shows a depression in each of these latter

[1] Anat. u. Physiol. fleischig verdickter Wurzeln, in Flora, Bd. lxiii, 1880. Compare especially his figures 1 and 2, of *Cochlearia*.

[2] Treub describes the formation of secondary vascular bundles from cells of the mature parenchyma in *Myrmecodia*, in which the primary bundle system perishes on the formation of the first internal periderm. From the account he gives it appears that the bundles may be formed from parenchyma, which is itself secondary (phelloderm), as well as from the primary ground-tissue. Treub, Sur le *Myrmecodia echinata*, in Ann. du Jardin bot. de Buitenzorg, T. iii, 1883, p. 139; Pl. xxii, Figs. 3, 4; xxiv, Figs. 8, 9, 10.

[3] l. c. p. 147. [4] l. c. p. 147. [5] l. c. pp. 259–263.

regions. Divisions then take place in the cells of the pericycle outside the phloëm-masses, and thus the normal cambium again forms a regular ring. The process is now repeated. Abundant wood is again formed opposite the primary bundles, while between them a smaller amount of wood and excessive bast is produced, until the cambium closes in a second time. This goes on indefinitely, and so the wood ultimately consists of alternating radial portions quite different in structure. The portions lying opposite the primary xylem-groups consist of normal wood, while the interfascicular regions are made up of successive tangential plates of non-vascular wood and of soft bast. There are four radial masses of each kind in *Thunbergia*. The process only differs from that in *Strychnos* in the facts that in the latter the xylem is of similar structure throughout, and that the phloëm-islands do not all lie in the same radial lines.

In *Goodenia ovata* Vesque[1] found that there is a normal ring of bundles, but as regards five of these the cambium is extrafascicular, the phloëm of these bundles thus becoming buried in the wood. This is a case of what may be termed primary phloëm-islands. It is not mentioned by Solereder under this head, as it obviously does not fall under his definition of interxylary phloëm, but from our point of view this case affords an interesting parallel to the process in *Strychnos* and the Acanthaceae.

Lastly we may mention the phloëm-groups in the xylem of the root of certain Onagraceae, Solanaceae, and Gentianeae described by Weiss[2]. These growths are formed directly from the cambium on its inner side. They never grow subsequently by means of a special cambium of their own, and thus differ from the similar groups in the root of *Salvadora*, and from the interxylary bundles in the roots of Cruciferae and Cucurbitaceae.

These last-mentioned bundles are formed sometimes in the parenchymatous part of the secondary wood at a distance from

[1] l. c. p. 146.

[2] Flora, Bd. lxiii, and Bot. Centralblatt, Bd. xv, p. 407.

the cambium, and sometimes in the pith. In the Cruciferae a group of phloëm is first formed, then a ring of cambium surrounding it gives rise to additional phloëm-elements on the inside, and to a little xylem on the outside[1]. According to Weiss, these concentric bundles are continuous with leaf-trace bundles of the stem[2].

In *Bryonia*, on the other hand, where the new formation takes place around a normal group of xylem, the phloëm lies externally, and the xylem internally, with reference to the special cambium[3]. These interxylary bundles are only indirectly connected with our immediate subject. They bear the same relation to true phloëm-islands as complete medullary bundles bear to the internal phloëm-groups of a normal ring of bicollateral bundles.

Summing up the results of our survey, we see that the few satisfactorily investigated examples of phloëm-islands are about equally divided between the centripetal and centrifugal modes of development. Thus Hérail's 'general law' above cited does not hold good universally, any more than does the opposite generalization of Solereder. Every case must be investigated on its own merits.

It is worth mentioning that interxylary phloëm-islands in the stem generally occur in connection with bicollateral bundles. According to Solereder, the exceptions to this rule are limited to the five genera *Dicella*, *Sarcostigma*, *Salvadora*, *Dobera*, and *Hexacentris*[4]. The same author finds that the occurrence of phloëm-islands is not so constant a character for large groups as is the presence of bicollateral bundles. This is quite what would have been expected *a priori*. Phloëm-islands are a secondary formation arising late in the development, while bicollateral bundles are part of the primary structure formed on the first differentiation of the tissues.

[1] See Figs. 1 and 2 of Weiss's paper in Flora.

[2] Bot. Centralblatt, xv, p. 407.

[3] Flora l. c. Figs. 5 and 6. By an oversight this is wrongly described in the text of the paper, p. 110.

[4] l. c. p. 33.

It is premature to speculate on the physiological significance of the structure we have been considering. There is certainly a tendency among many Dicotyledons (both climbers and others) to find a more protected position for their conducting tissues than is provided by the typical orientation of wood and bast. To take only two familiar examples: In *Bignonia* all the larger sieve-tubes are contained in the phloëm-plates which are so well shielded by the wood. The sieve-tubes of the external phloëm are comparatively insignificant. Similarly in *Tecoma grandiflora*, and no doubt in some of the other species, the medullary phloëm is better developed than the normal. In this plant the medullary wood is also characterized by its large and numerous conducting elements. Whether the internal position of the conducting, and especially of the proteid-conducting tissues offers any other advantage than that of protection must be left an open question for the present.

Although, as we have seen, Hérail's generalization as to the uniform character of the tissue produced on the same side of the cambium, is not constantly true, yet we now know that in the great majority, even of the anomalous cases, the cambium forms phloëm centripetally and xylem centrifugally. The wood of *Strychnos* was compared by de Bary and van Tieghem[1] with that of the Chenopodiaceae, and the comparison still holds good, though the order of development in both is different from what they supposed. As is well known, the wood of the Chenopodiaceae, Nyctagineae, Phytolaccaceae, and Aizoaceae shows, within the cambium, concentric rings of collateral vascular bundles, imbedded in secondary ground-tissue, which is itself often lignified. In some cases successive cambial rings appear; in others the secondary collateral bundles appear to be all formed by one and the same ring of cambium. According to de Bary's account, the phloëm of these bundles is formed from an initial strand, separated off internally from the cambium[2], so that in

[1] l. c. p. 797.

[2] l. c. p. 592.

this numerous class of cases the phloëm-formation appeared to be centrifugal. Morot[1] was the first to show that in various Chenopodiaceae, Nyctagineae, etc., in fact throughout the families in question, the cambium constantly gives rise on its inner side to the wood of the bundles, on its outer side to their bast. The generative zone always passes *between xylem and phloëm*, but only has a temporary activity. In order that other more external bundles may be formed, it is necessary for new generative zones to be produced outside the first one. These new cambial zones may either be entirely distinct from their predecessors, or, as is more frequent, may have more or less numerous points of contact with them. In the latter case the original generative zone may maintain its activity in the intervals between the bundles, but these interfascicular cambial arcs become connected by bridges of meristem passing outside the bast, and destined to replace the generative arcs interposed between phloëm and xylem. As Morot points out, it is the persistence in some cases of the activity of the interfascicular portions of the cambial ring, which led to the belief that the activity of the entire ring is persistent. Thus to Morot belongs the credit of showing that the activity of each cambial ring is perfectly normal throughout the whole of this series.

The conclusions of Morot have been fully confirmed by Hérail[2], Strasburger[3], Petersen[4], and by the independent observations of one of us on *Mirabilis*, *Bougainvillea*, *Chenopodium*, *Amarantus*, and *Mesembryanthemum*. In all these cases, while the bulk of the secondary tissues is formed centrifugally, the phloëm of each bundle is developed, as in normal cases, centripetally.

It is to be regretted that the recent authors Gheorgieff[5],

[1] Recherches sur le péricycle, in Ann. des Sci. Nat. Sér. vi, T. xx, 1885, p. 284.

[2] l. c. p. 247.

[3] Das botanische Practicum, 2te Auflage, 1887, p. 170.

[4] Staengel-bygningen hos *Eggersia buxifolia*, in Botanisk Tidsskrift, Bd. xvi, French résumé, p. 9.

[5] Beitrag z. vergl. Anat. d. Chenopodiaceen, in Bot. Centralblatt, Bd. xxx and xxxi, 1887.

Heimerl[1], and Pax[2], who have worked at the anatomy of these families, appear to have paid no special attention to the development. Some of Gheorgieff's figures, however, in Pl. VI and VII of his paper, leave no doubt as to the centripetal development of the phloëm in the plants he examined. He describes and figures obliteration of the phloëm here, similar to that which we have so often mentioned in *Strychnos*.

The phloëm-islands of *Strychnos*, then, in their centripetal development from the cambium, conform to a law of wide though not of universal application.

The occurrence of medullary phloëm in the root affords one more decisive argument that the vascular cylinder of the root should no longer be described as a single vascular bundle, but should be regarded as corresponding to the whole vascular system and pith of the stem.

The material for our investigation was supplied partly from the Royal Gardens at Kew, partly from the Garden of the Society of Apothecaries at Chelsea, and to the heads of both these institutions we tender our thanks. We wish further to thank both the Kew authorities and those of the botanical department of the British Museum, for valuable help in the identification of species.

Some of the preparations, including that from which Fig. 1 is drawn, were made by Miss A. L. Smith, whose help we have pleasure in acknowledging.

[1] On Nyctagineae in Engler u. Prantl's Die natürlichen Pflanzenfamilien, Theil III, Abth. 1, 1889.

[2] On Aizoaceae. Ibidem.

EXPLANATION OF FIGURES IN PLATES XVIII AND XIX.

Illustrating Messrs. Scott and Brebner's paper on *Strychnos*.

The following lettering is used throughout:—

cb^1 = Normal (including complementary) cambium.
cb^2 = Medullary cambium, adding new elements to the medullary phloëm-groups.
cb^3 = Cambium from which the phloëm-islands are produced.
ph^1 = Normal external (rudimentary) phloëm.
ph^2 = Medullary phloëm.
ph^3 = Phloëm-islands, ultimately imbedded in the wood.
x^1 = Primary xylem.
x^2 = Secondary xylem.
pc = Pericycle.
p = Pith.
lp = Lignified pith.
r = Medullary ray.
c = Companion cell.
s = Sieve-tube.

Fig. 1. *S. spinosa*, Harv. ×500, transverse section. Young vascular bundle, showing external phloëm-groups, and the medullary group in course of formation.

Fig. 2. *S. spinosa*, ×920, transverse section. External phloëm-groups at a slightly older stage. The sieve-tubes (with sieve-plates) and companion cells are shown. Only young unlignified xylem is shown.

Fig. 3. *S. spinosa*, ×920, longitudinal section. At the same stage as the last, showing a sieve-tube and companion cell in an external phloëm-group. A nucleus is present in the sieve-tube.

Fig. 4. *S. nux vomica*, L., × 333, transverse section. Shows a medullary phloëm-group. On its outer side is an active cambium, while on the inner side the elements are beginning to become obliterated.

Fig. 5. *S. nux vomica*, × 333, transverse section. More advanced medullary phloëm-group. The cambium is ceasing its activity, and a great mass of obliterated elements is seen on the inner side.

Fig. 6. *S. nux vomica*, × 333, transverse section. First commencement of the formation of a phloëm island. The normal cambium is increasing its activity in this region, and has already produced a few sieve-tubes and companion cells. The compressed elements *may* be primary phloëm. No retardation of wood-production is as yet to be noticed. This is from an old stem (thickness 5 mm.).

Fig. 7. *S. nux vomica,* × 333, transverse section. More advanced stage. The phloëm-cambium is now quite detached from the normal ring. The obliteration of peripheral elements is making progress. The island is now deeply sunk in the wood.

Fig. 8. *S. nux vomica,* × 500. Longitudinal radial section of a phloëm-island at a similar stage. The cells of the special phloëm-cambium are shown with contents. Sieve-tubes and companion cells are shown.

Fig. 9. *S. nux vomica,* × 333. Transverse section at a later stage. The phloëm-island is now overtopped by xylem on either side, and divisions in the bast-parenchyma have completed the normal cambial ring outside the island. The phloëm-cambium is in full activity, and the continuity of the radial rows of phloëm-cells with those of the internal xylem is especially evident here.

Fig. 10. *S. nux vomica,* × 333. Slightly later stage. The wood is now beginning to close in on the outside of the phloëm-island. The number of obliterated peripheral elements in the latter has increased, but the cambium is still as active as ever.

Fig. 11. *S. nux vomica,* × 333. Very old phloëm-island, completely immersed in wood. An immense mass of obliterated elements is seen on the outside. The cambium shows but little signs of activity. This corresponds to Fig. 5 of the medullary phloëm.

Fig. 12. *S. spinosa,* × 333. Transverse section of root, in which secondary thickening has begun. A medullary phloëm-group is seen in the pith opposite a group of primary xylem. These groups increase slightly by an external cambium as in the stem. Thickness of root about 4 mm.

Note.—Figs. 4, 5, 6, 7, 9, 10, 11, and 12 were drawn under a power of 500 diam. and subsequently reduced to two-thirds.

Fig. 1.

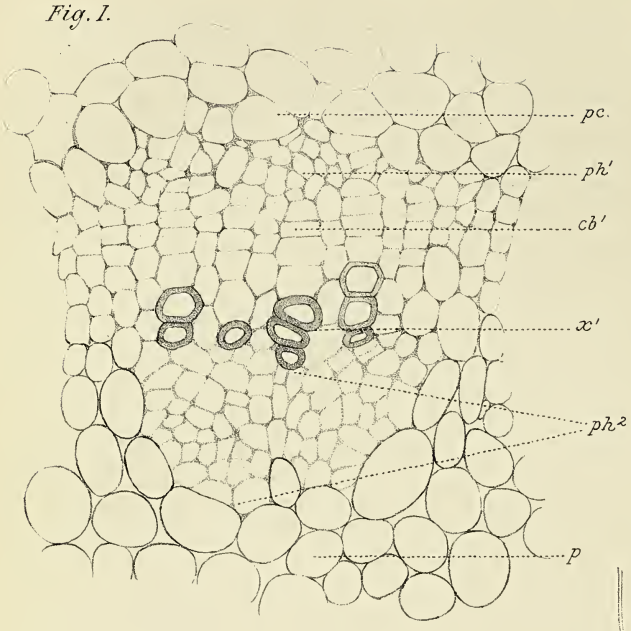
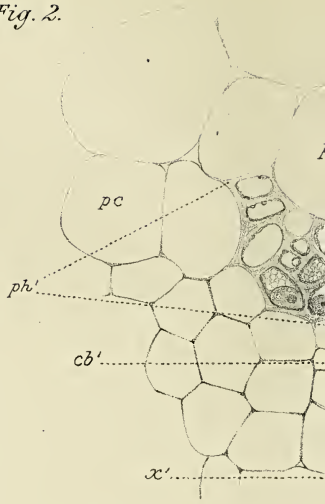


Fig. 2.



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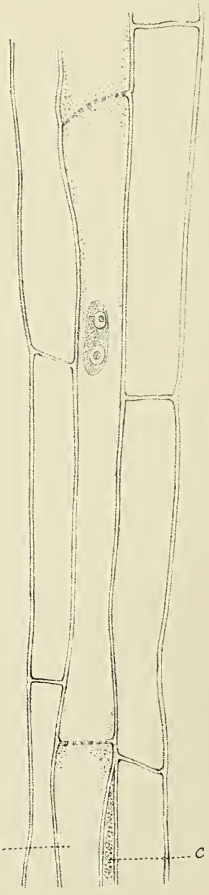


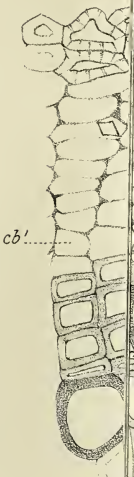
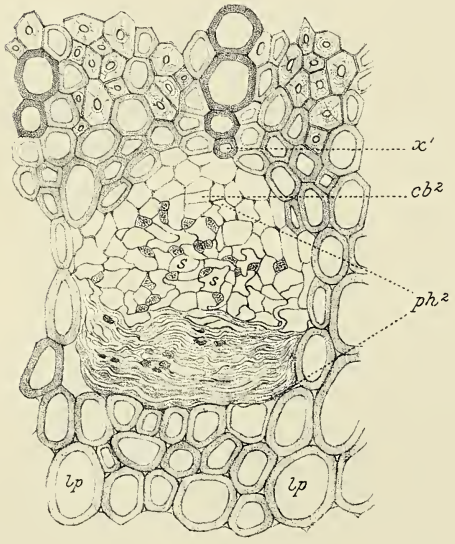


Fig. 5.



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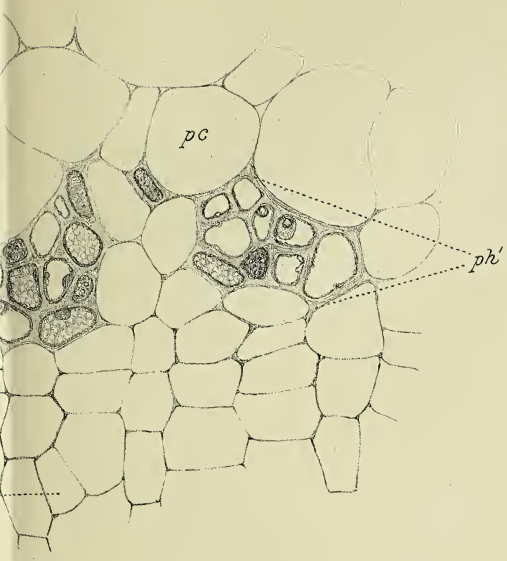

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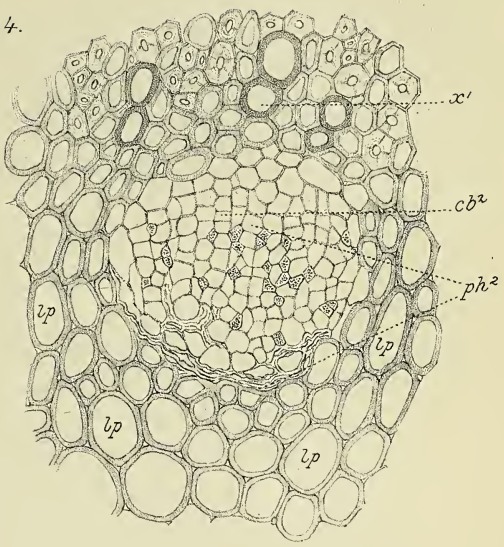

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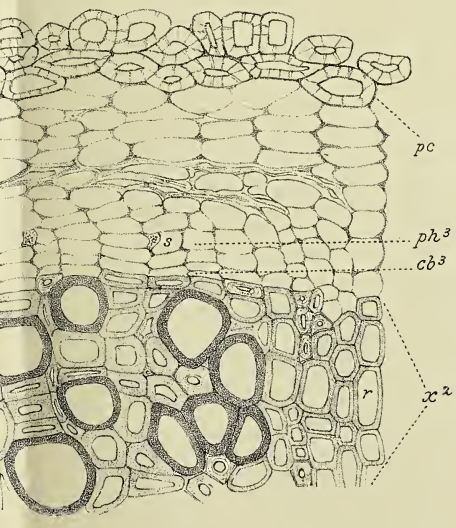

Fig. 7.

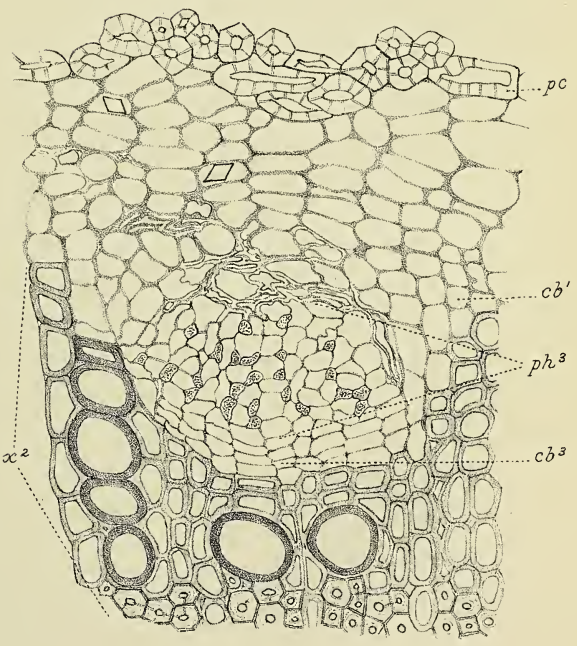

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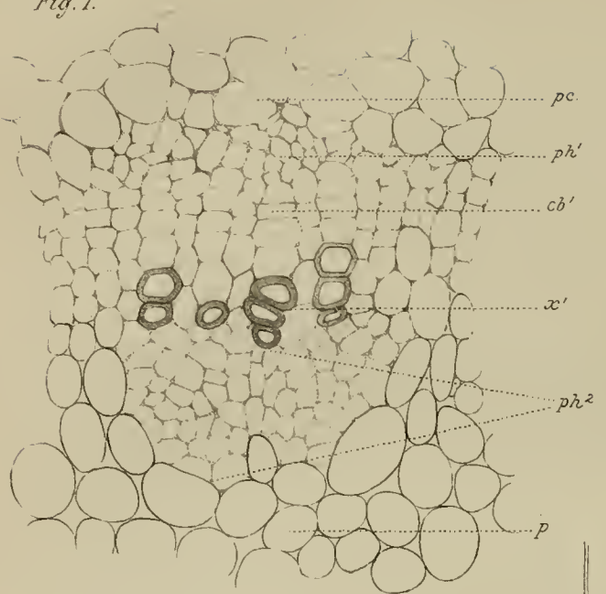
Fig. 1.



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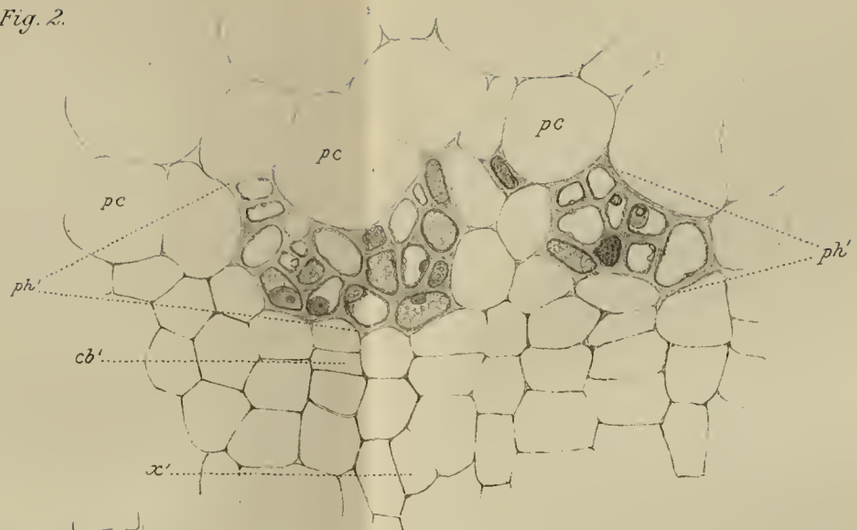

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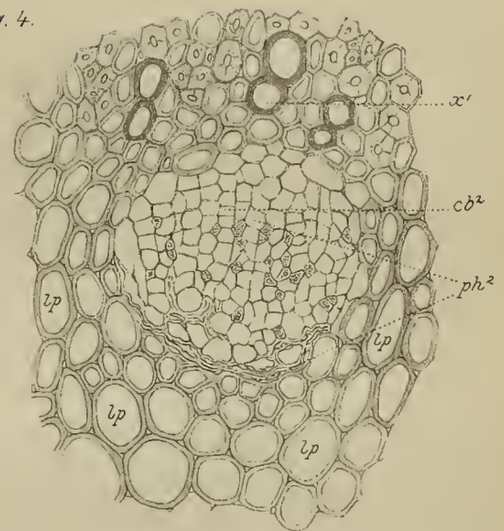

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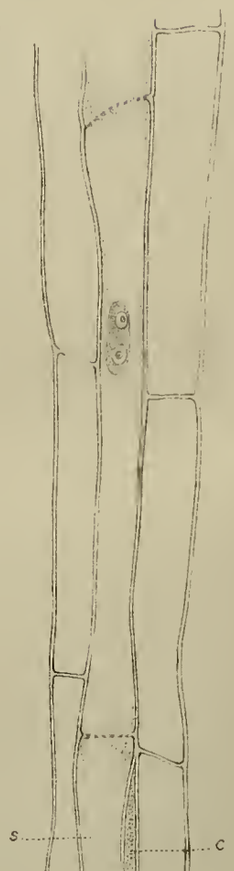

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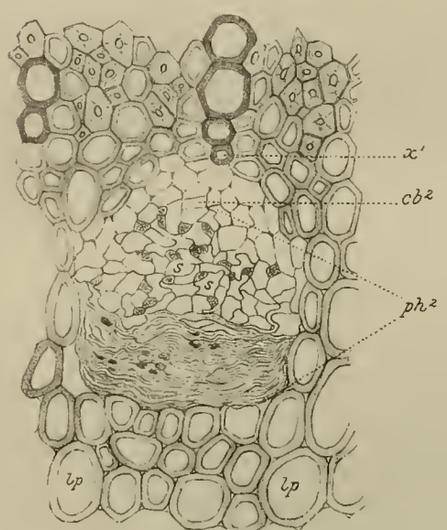

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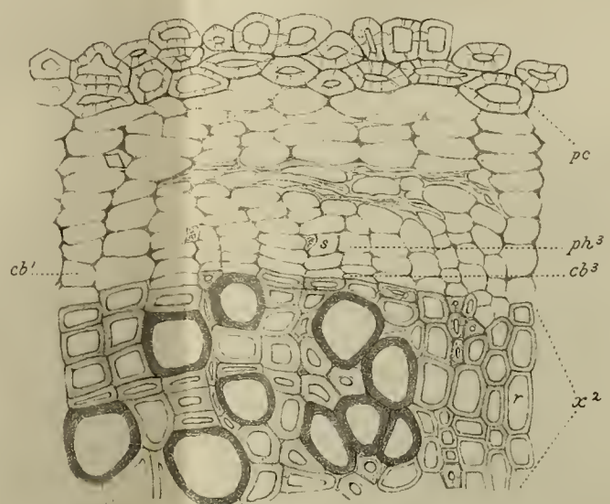
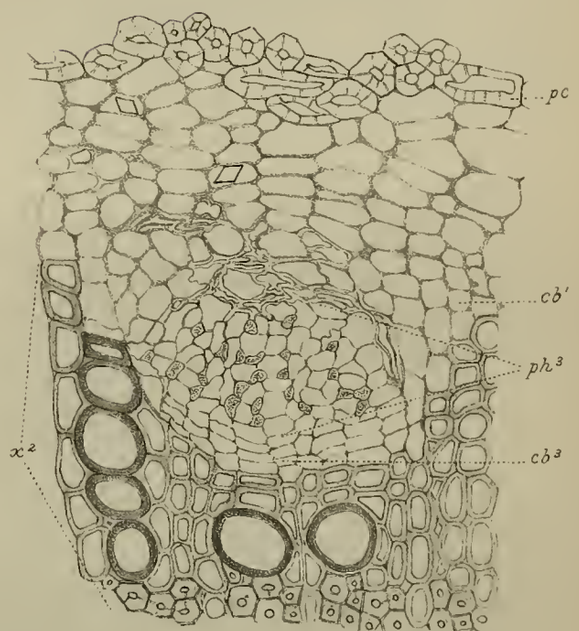


Fig. 7.



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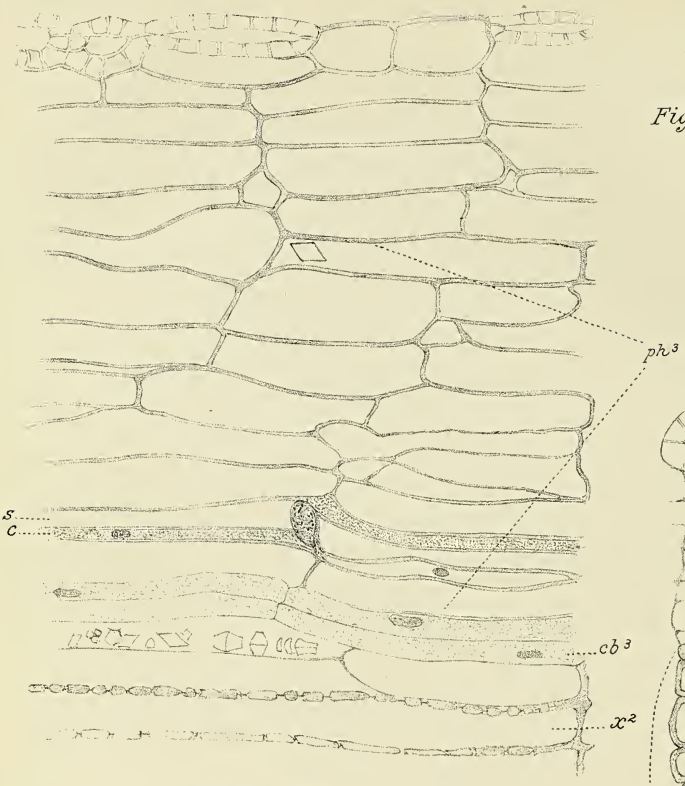
SCOTT AND BREBNER.— ON THE ANATOMY OF STRYCHNOS.



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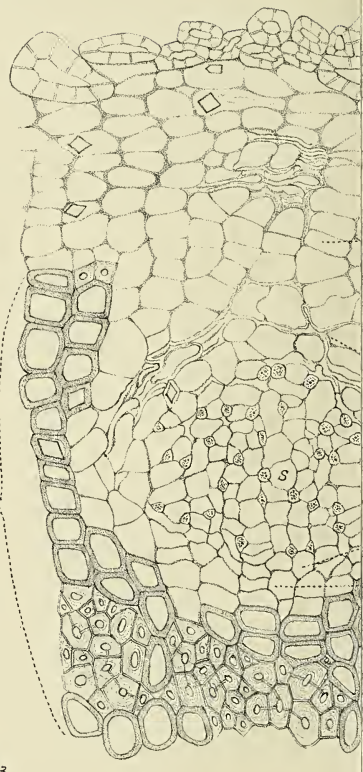

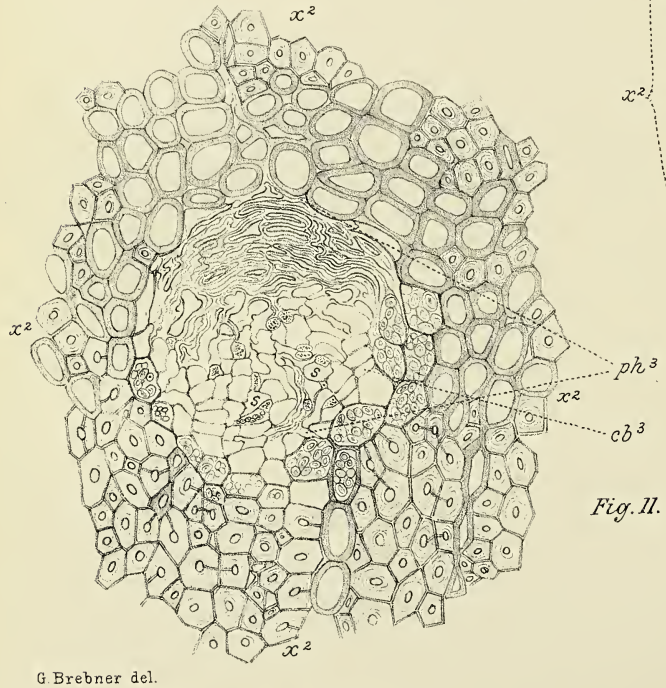

Fig. II.

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Fig. 10.

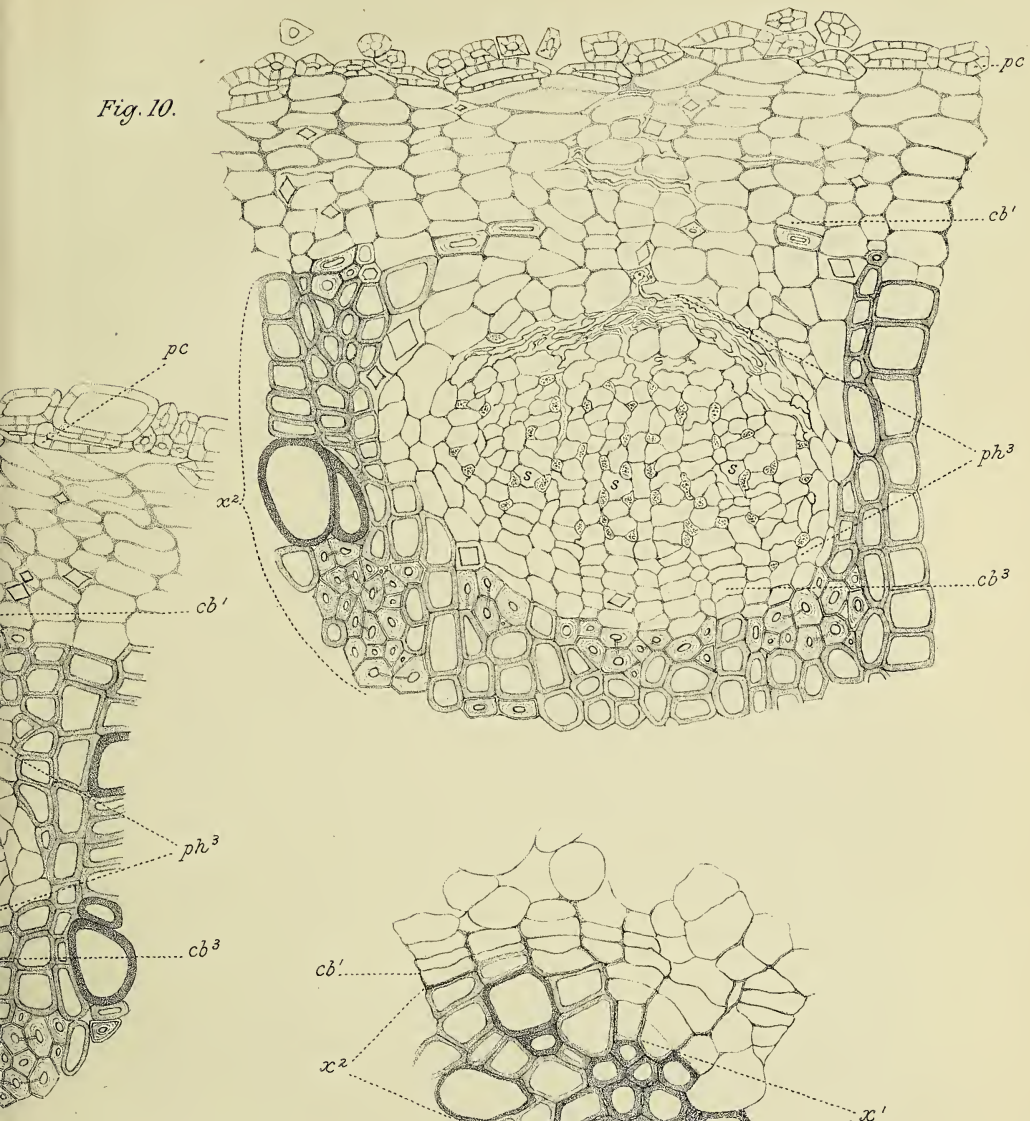

Fig. 12.

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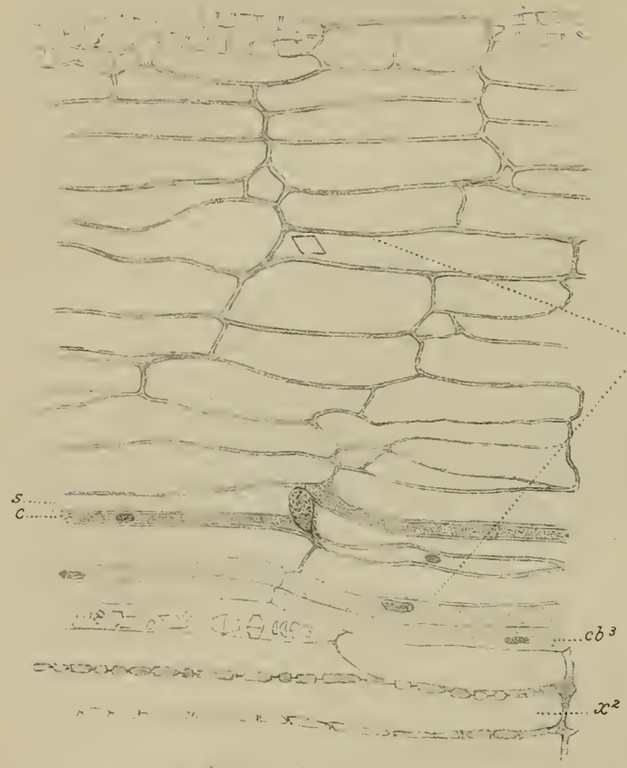

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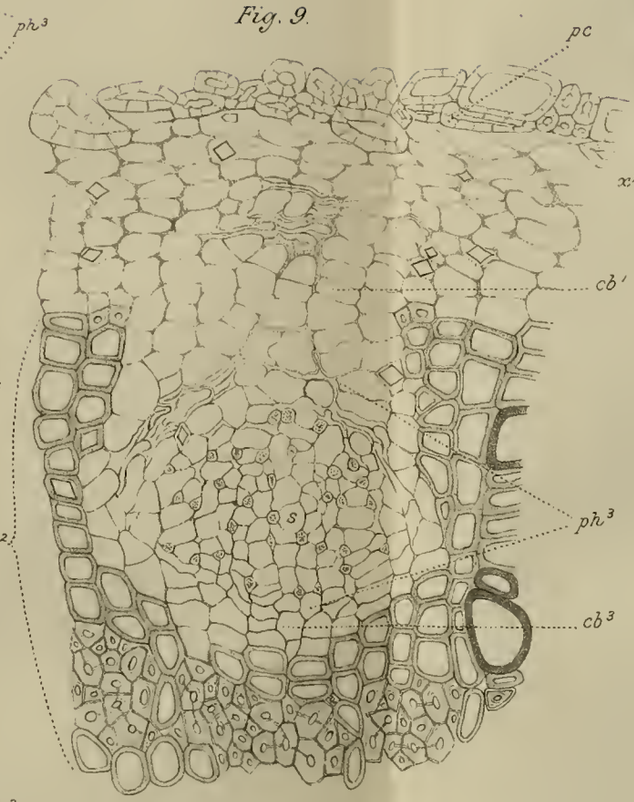

Fig. 9.

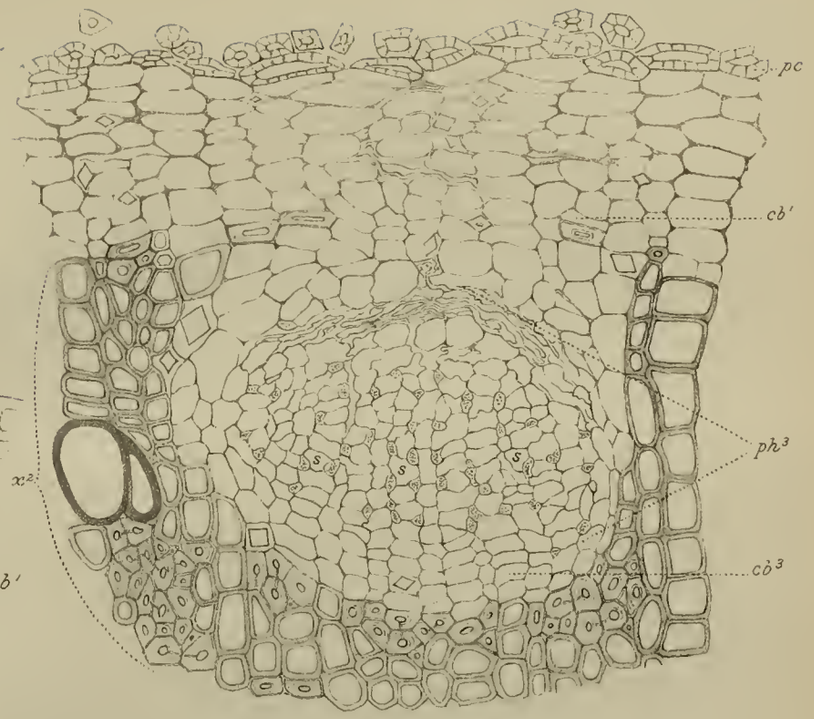

Fig. 10.

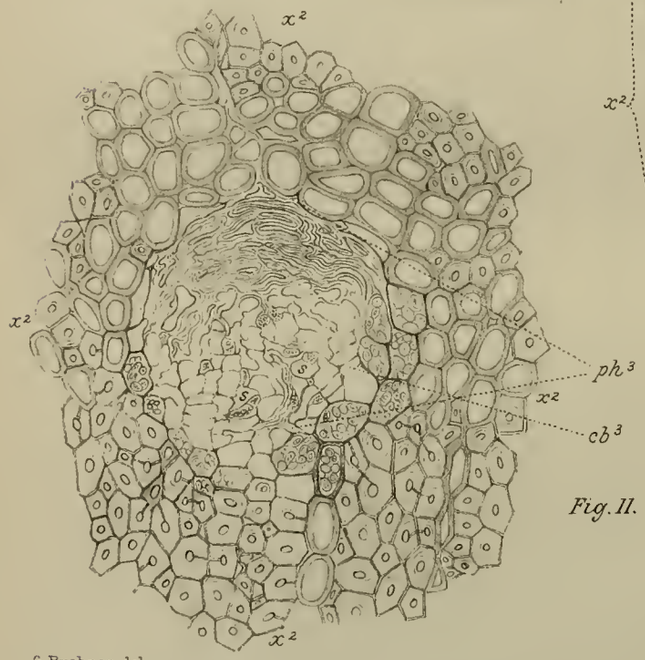

Fig. 11.

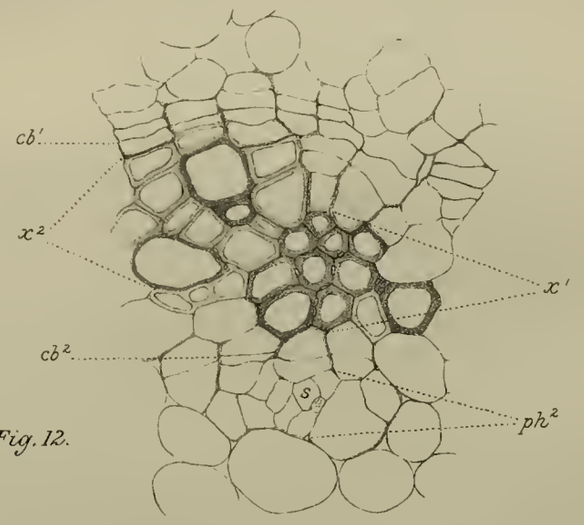

Fig. 12.

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SCOTT AND BREBNER.— ON THE ANATOMY OF STRYCHNOS.

The comparative examination of the meristems of Ferns, as a Phylogenetic Study.

BY

F. O. BOWER, D.Sc.

Regius Professor of Botany in the University of Glasgow.

With Plates XX, XXI, XXII, XXIII, and XXIV.

Introductory Remarks.

IT is the ultimate aim of all working morphologists who entertain a view of evolution in one form or another, to reconstruct as nearly as possible from the fragmentary records at our disposal the developmental tree. All must however feel that not only is the series too greatly broken to allow of launching out with certainty upon definite views as to the exact relation of existing forms, but also that our knowledge of the details of structure and development of many of the organisms we see living before us is too slight to provide sound ground for argument. At the same time, no details are to be considered as too trivial provided their value be not over-estimated. It is the interest and the duty of investigators at present to attempt to build up short branches of the main tree, rather than to hazard guesses as to the relation of organisms which are but remotely connected; by careful investigation to arrange the more closely related organisms serially according to their characters, in the hope that this may lead to the affinities of such series to others being the more clearly recognised at

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either one end or the other. More especially is it desirable that such series should be as strictly defined as possible in those parts of the organic system which obviously lead as connecting links from the lower to the higher, and in no part of the vegetable kingdom is such definition more necessary than in the Vascular Cryptogams. These are admitted to be a transition series from the simpler forms of Algal-Bryophytic affinity to the Phanerogams. It is now generally accepted that there have been at least three series of the Vascular Cryptogams, which after their first origin developed independently of one another: viz. the Lycopodineae, the Equisetineae, and the Filicineae; the more clearly we are able to parcel out the members of these series according to their true affinities among themselves, the less complex will the problem become of recognising the relations of the series one to another, and their connection severally with the forms lower or higher in the main series of plants.

It is reflections such as these which have led me from time to time to devote attention to the Filicineous series of Vascular Cryptogams, and it is the object of the present pages to give a general account of the characters of the meristematic tissues of root, stem, leaf, and sporangium in a number of these plants. Many facts regarding them are already well known, and these, together with freshly acquired facts, will be found sufficient to demonstrate that even in a character so apparently special as the structure of the meristematic tissues, these plants form a natural series.

The distinction between eusporangiate and leptosporangiate forms, according as the sporangium is derived from a single cell or from a group of cells, was first emphasised by Goebel[1], and it has been generally adopted. It will be shown, however, and Goebel himself contemplates this as possible[2], that this distinction cuts in two what is obviously a natural and continuous series: that though it is useful to recognise the difference between plants in which the sporan-

[1] Bot. Zeit. 1881, p. 717.

[2] Schenk's Handbuch, III, p. 387.

gium originates only from a single cell, and those in which it has a pluricellular origin, it would be a mistake to accentuate this distinction, for it will be seen below that the Filicineous series leads from the one type to the other by gradual steps, and it is only among Filicineae that leptosporangiate forms are known. Further, it will be shown that as we pass along the series of Ferns from the leptosporangiate to the eusporangiate forms, an increase of complexity of structure more or less marked is to be seen, not only in the sporangium, but in every one of the meristematic tissues: in fact, that the progress in complexity from the leptosporangiate to the eusporangiate Ferns not only involves the increased bulk and robustness of the sporangium, but may be taken as an indication of a more bulky type of development of all the parts of the plant: it will be shown that just as in passing along the series the sporangium of unicellular origin in the Hymenophyllaceae and Polypodiaceae becomes the massive sporangium of *Marattia*, so also as we review the series, we pass from the root with one clearly defined apical cell to that with several initials, while a similar transition from a simple to a more complex construction is to be noted in the apices of stem, and leaf, and even in the mode of origin of the wings of the leaves.

The above remarks will suffice to indicate the general scope of the present memoir: the theoretical considerations which will follow from this comparative study of the meristems of Ferns will be deferred to the concluding paragraphs.

In order to bring out the more clearly the fact that the progress from the simpler to the more complex is exemplified in each of the meristems of root, stem, leaf, wing, and sporangium, each of these parts will be dealt with separately, and their characters traced in a series of examples, and it may be stated that, with few exceptions, the same species have been used for the investigation of each of the above-named parts. So as to preserve some uniformity of treatment, the forms investigated will be taken in regular sequence; the Hymenophyllaceae first, because of their greater simplicity of con-

struction ; then the rest of the leptosporangiate Ferns[1], with the Schizaeaceae as a group leading towards the Osmundaceae, which in turn lead on to the Marattiaceae.

The material necessary for this investigation is for the most part rare : the specimens of *Trichomanes* and *Hymenophyllum*, as well as some others, have been supplied from Kew, and I wish to record my thanks to the Director of the Royal Gardens for this, and for the use of the Jodrell Laboratory, in which much of this work was conducted. Other specimens were derived from the Glasgow Garden, while the specimens of *Marattia* and *Angiopteris* were from my collections made in Ceylon.

Apices of Roots.

I am not aware that any observations of the structure of the apex of the root in any of the Hymenophyllaceae have been recorded, beyond the remark of Prantl[2] that one conical apical cell is present in *Gonocormus* (*Trichomanes*) *dichotomus*, which he figures in longitudinal optical section in his Plate I, Fig. 8. I have had the opportunity of observing the apex of the roots of *Trichomanes radicans*, and of *Hymenophyllum demissum* : in both of these the structure was found to conform to the normal type for the root of leptosporangiate Ferns, as described by Naegeli and Leitgeb[3], and accordingly there is no need here for a special description or for figures : it may, however, be remarked that the structure as shown in Prantl's Fig. 8, above quoted, does not convey the impression of the exact sequence of the cell-divisions being normal ; but as the figure was drawn, not from a section, but from an apex cleared by reagents, and seen in optical section, the slight discrepancy need be no obstacle to the conclusion that the

[1] I do not think it necessary for the present argument to arrange these leptosporangiate Ferns in any definite sequence, since their relation to one another is still uncertain, while the construction of their meristems appears to be almost uniform.

[2] Unters. z. Morph. d. Gefässkrypt. Heft I, p. 31.

[3] Beitr. z. wiss. Bot. Heft IV, 1868.

typical apex of the root of Hymenophyllaceae is coincident in structure with that of other leptosporangiate Ferns.

The apex of the root has been investigated in a large number of other leptosporangiate Ferns: e. g. by Naegeli and Leitgeb (l. c.) in *Asplenium Filix-foemina*, *Pteris aquilina* and *hastata*, *Platycerium alcicorne*, *Blechnum occidentale*; by Hofmeister in *Aspidium Filix-mas*[1]; by Hanstein in *Marsilia*[2]; by Strasburger in *Pteris cretica*[3], and in *Azolla*[4], etc., etc. I have also myself investigated the apices of roots of *Cyathea insignis*, Eat., *Gleichenia circinata*, Sw., *Gl. flabellata*, R. Br., *Gl. rupestris*, *Lygodium scandens*, *Aneimia hirta*, and *Phyllitidis*, and *Pilularia globulifera*. It will be seen that among the plants above noted there are representatives of all the families of leptosporangiate Ferns, including the Hydropteridеae: in all of them the organic apex of the root conforms in structure to the type laid down by Naegeli and Leitgeb: all have a single, three-sided, pyramidal apical cell, from the sides of which segments are cut off in regular succession by walls parallel to the three sides, and these are formative of the body of the root: after each series of three such segments a fourth is cut off from the base of the pyramidal cell, and such segments are formative of the root-cap. This type of construction has been represented diagrammatically by Sachs[5] in a figure which is here reproduced (Fig. 1): in this it is to be noted that the centre of construction (S) of the whole system of curves lies within the apical cell itself, and that the whole (exclusive of the root-cap) falls under that series of systems of construction which are designated as *confocal*[6]: there may be slight variations in detail of the succession of the segmentations; thus Kny notes

[1] Higher Cryptogamia, Ray Soc. Plate XXVI.
[2] Pringsh. Jahrb. IV, p. 230. [3] Practicum, p. 278.
[4] Ueber Azolla, p. 45.
[5] Arbeiten d. Bot. Inst. Würzb. Bd. II, Taf. IV, Fig. 12.
[6] Compare Sachs' Lectures, Clarendon Press, 1887, p. 451. The term 'confocal' applies properly to the body of the root only, the root-cap being coaxial: but still this type may for brevity be termed confocal to distinguish it from that in which the construction of the body of the root is coaxial.

in *Ceratopteris*[1] that the succession of three segments from the sides and then one from the base is not strictly maintained, but that the number of segments cut off from the sides is considerably greater than three to each segmentation from the base: differences of detail may also be noted in the further subdivision of the segment; but still, putting aside these exceptions, the type for the roots of all the leptosporangiate Ferns, including also the Schizaeaceae, seems to be quite clearly definite, and constant. This uniformity of structure makes those deviations from that type, which will now be described for the roots of the Osmundaceae, more noteworthy than they would otherwise appear.

An examination of the apex of the root of the Osmundaceae has shown that its structure does not conform strictly to this simple type of the leptosporangiate Ferns, while there is considerable variation in detail, even in different roots taken from the same individual plant. Among the many roots of *Osmunda regalis* which I have examined, some few show a certain similarity in the confocal type: thus in transverse sections a single three-sided pyramidal apical cell may occasionally be found; but even when this is the case the structure does not show that diagrammatic regularity which is so characteristic of the roots of the leptosporangiate Ferns (Fig. 2). Other roots of *Osmunda* show in transverse sections other irregularities, such as a single four-sided apical cell, or two such four-sided initial cells, etc.; but of all the aberrant modes of arrangement of the cells of the apical meristem found in the roots of *Osmunda regalis*, that which is most interesting from a theoretical point of view is that represented in the Figs. 3, 4. In these figures it may be seen that the whole tissue is referable in its origin to three initial cells, which are marked (x), while the three walls separating these cells from one another meet at a central point. These three walls are drawn in heavier lines in the figures, and may be traced for some distance from the central point: they may be called the principal walls. In each case the portion of tissue derived from one of these initial cells is

[1] Parkeriaceae, p. 48.

enclosed between two of these principal walls, and thus the whole meristem may be regarded as consisting of three wedge-shaped masses. Taking now those masses singly into consideration, it will be clearly seen that in Fig. 3 each is divided into two unequal parts by walls marked (*s*), which do not proceed to the centre, but on passing towards it curve gradually out of the radial plane, and insert themselves at right angles on the principal walls: these may be called the sextant-walls. A similar arrangement, but less clearly marked, may be seen in such examples as that represented in Fig. 4. In each case the error of regarding sections below the real initial cell or cells as including the initial cells, has been carefully avoided by comparing the whole series of sections cut from each individual root.

For comparison with this arrangement of the initial cells and their derivatives I have quoted as Fig. 5 one of the drawings of Naegeli and Leitgeb, which appeared in their well-known work, 'Entstehung und Wachsthum der Wurzeln,' as Taf. XII, Fig. 8. This represents a view of the structure seen immediately below the apical cell in the root of *Pteris hastata*, and it will be seen that in the most essential points the structure of its central portion is similar to that in Figs. 3 or 4: and if we imagine these principal (*p*) and sextant-walls (*s*) to be continued upwards in Pteris or any leptosporangiate Fern, till they reach the root-cap, a structure of the root-apex would result which would correspond to that observed in certain cases in *Osmunda regalis*: in other words, accepting the view of Sachs that the apical cell is a gap in the system of construction, such roots as these of *Osmunda regalis* show the gap less complete, and the three principal walls continued through it, so as to divide it into three parts.

Since the characters of the meristem in the root of *Osmunda* have thus been shown to be subject to variation, and since it is hardly possible to determine with certainty from longitudinal sections what is the actual number and form of the initial cells, a full and exact interpretation of the structure in longitudinal sections cannot be expected. In the majority of

cases, cells of a pyramidal form have been found occupying an approximately central position in median sections: but in no single instance has an apical cell been observed having that regularity of form, and of the arrangement of its segments, together with the central position, which are so characteristic of the roots described by Naegeli and Leitgeb. Taking as the first example (Fig. 6) one of those which approaches most nearly to that type, the pyramidal apical cell (x) can be readily recognised; but a comparison with the figures of Naegeli and Leitgeb, or with Fig. 1, shows certain points of difference. In the first place there is a difference in the form of the cell itself; it is in *Osmunda* proportionately narrower and deeper, that is, more elongated in a longitudinal direction, and consequently the principal walls by which it is bounded laterally are less inclined to the longitudinal axis. Secondly, the arrangement of the cells surrounding the pyramidal cell does not show any definite regularity, and it is thus difficult to ascertain their genetic connections. This irregularity is found not only in the tissue adjoining the sides of the pyramidal cell, but also in those which have been derived from its base, and will go to form tissues of the root-cap. This, it may be stated, is one of the most regular examples of the apex of the root of *Osmunda* which I have observed.

A further point to be noted in Fig. 6, as also in Fig. 7, is that in point of size the wedge-shaped cell is smaller in comparison with the adjoining cells, than is the case in other Ferns: whereas in Naegeli's figures the area of the apical cell equals or exceeds that of any of the surrounding cells, in *Osmunda* it is often smaller than they. In the apex represented in Fig. 7, a central pyramidal cell is clearly seen: here, though there is no marked ascendancy of the neighbouring cells in point of size, still if the genetically connected groups of cells, enclosed between the successive anticlinal walls be taken into consideration as products of successive segments, it is clear that the construction here differs considerably from the ordinary confocal type; the ascendancy of the apical cell is less marked, and periclinal walls predominate, while the anticlinal

walls present a distinctly convex internal surface: thus while in this root a cell is present which may be recognised as a pyramidal apical cell, the whole construction approaches that of the co-axial or fan-like type.

Lastly, the less common, but very interesting arrangement shown in Figs. 8 and 9 must be mentioned. Here no pyramidal cell is to be found; the median longitudinal section shows two cells (*x*, *x*) of truncated pyramidal form, from which segments are cut off, (1) from the base, to form tissues of the root-cap; (2) from the sides, and (3) as shown in Fig. 8, from the truncated apex also. In this case the correspondence with Schwendener's description [1] of the apical group in the root of the Marattiaceae is very apparent.

It has been demonstrated repeatedly by various authors that in the cases of *Equisetum* and many Ferns there is a certain order of succession and regularity of position of those walls by which the segments are divided up into smaller cells. A comparison of the drawings above quoted, with those of Naegeli and Leitgeb, will suffice to show that in *Osmunda* the outer limit of the procambial cylinder does not appear to correspond to any definitely recurring wall in the young segments, as is the case in the roots investigated by Naegeli. The same may be said with respect to the limits of the cortex and epidermis; the latter tissue, which can readily be recognised in the older part of the root, and can be traced as entering below the layers of the root-cap, loses its identity at a considerable distance from the actual organic apex of the meristem. This fact is illustrated in the Figs. 6 and 9: in neither of these examples can a clear distinction be drawn between those cells which will develop as tissue of the root-cap and those which will form epidermis or cortex.

The results now detailed have been further supported by observations on young developing lateral roots: in Fig. 10 is shown a young lateral root in median section, and here are seen two oblong initial cells which accord in form and position to those shown in Fig. 8, while the case of Fig. 11 shows a

[1] Sitz. d. K. Preuss. Akad. d. Wiss. 1882.

single pyramidal cell narrower than that of Naegeli's type, and corresponding in many points to that of the older root shown in Fig. 6.

For comparison with *Osmunda regalis* the roots of *Todea barbara*[1] were investigated with the following results: Of a number of apices from which transverse sections were cut not one showed a clearly marked single apical cell. Some, however, showed somewhat irregular arrangements, and in some of these it appeared uncertain whether the meristem be referable to three or to four initial cells. In a majority of the roots observed it is clearly referable to four initial cells (Fig. 12), separated from one another by the four principal walls (p). The meristem in this case appears closely similar to that described by Schwendener in the Marattiaceae. Longitudinal sections, however, do not show so close a correspondence to the structure described by him in this group. Pyramidal cells are not unfrequently to be found, as in Fig. 13, where two are seen (x, x). In other examples, however, the initial cells have the form of truncated pyramids, as in Fig. 14, segments being cut off from the truncated apex, as well as from the sides and base. This arrangement probably corresponds to that shown in transverse section in Fig. 12.

The origin of the lateral roots was also observed in this plant. The root originates from a single cell of the endodermis, situated opposite one of the groups of xylem. Usually the divisions are symmetrical, as in Figs. 15, 16, and these two figures show that from the very first the initial cells of the young root are subject to a certain variation of form, being in some cases pyramidal, in others truncated. Thus, in this respect again, *Todea barbara* resembles *Osmunda regalis*.

The foregoing description of the structure of the apical meristem of the roots of *Osmunda* and *Todea* shows that there is no such strict uniformity in these plants as is found in the meristem of the roots of typically leptosporangiate

[1] See postscript, p. 388.

Ferns. If, on the other hand, a comparison be drawn between the structure in the Osmundaceae, and that described by Schwendener for the Marattiaceae [1] it will be seen that in the character of the meristem the family of the Osmundaceae fluctuates between the two types, and affords intermediate examples between them. In order to make this point clear a comparison may be drawn between Sachs' diagram of the type of the Polypodiaceae (Fig. 1) and a diagram which I have constructed with the intention of representing the Marattiaceous type (Fig. 17). In the former the periclinal walls in the body of the root constitute an interrupted series of confocal paraboloid surfaces, their common focus or centre of construction being situated in the apical cell itself: the periclinal walls in the root-cap constitute a series of similar curves which are however not confocal, though they are coaxial. Since the anticlinal walls cut the periclinals at right angles, those in the body of the root present a concave surface to the axis of growth, while those in the root-cap, cutting the coaxial curves, present a convex surface.

In the Marattiaceous type, according to the description given by Schwendener (and my own observations on the roots of *Marattia fraxinea* and *Angiopteris evecta* bear out his conclusions rather than those of Russow [2]), the arrangement differs from the above type in certain important points, and a diagram may be drawn to show the scheme of construction as in Fig. 17. In this type of construction there are in the first place walls in two radial planes, which cut one another at right angles, and their line of intersection [3] is the organic axis of the root. The periclinal walls are none of them confocal, neither those which lie in the body of the root, nor even those in the procambial cylinder; they are, however, all coaxial, and their common axis is the line of intersection of the radial walls, that is the organic axis. As a necessary consequence

[1] l. c.

[2] Vergl. Unters. p. 107, Fig. 158. Compare also De Vriese and Harting, Monographie des Marattiacées, Fig. 27.

[3] As a matter of fact the two planes do not cut one another accurately along one line; this has been noted by Schwendener.

of this it follows that the anticlinal curves all present a convex surface to the axis of growth, there being no distinction in this respect between the root-cap and the body of the root. In fact the construction of the root is throughout on the coaxial or fan-like plan distinguished by Sachs [1]. It is further to be noted in connection with the scheme represented in Fig. 17, that the apparently transverse walls, by which successive segments are cut off from the lower ends of the truncated pyramidal initial cells, form part of the series of periclinal curves; and that the focus of each successive periclinal, by which segments are cut off from the initial cells to form the body of the root, lies at *the time of segmentation at a point below the group of initial cells.* In the former type, however (Fig. 1), it will be readily seen that the focus or centre of construction lies in the apical cell itself (Sachs, l. c.). Thus in passing from the first to the second type of construction, there is a sinking or lowering of the centre of construction; since the anticlinals cut the periclinal curves at right angles, it follows that where the centre of construction is more depressed, the sides of the apical cell or of the initial cells will be less inclined to one another, and more nearly parallel than is the case where the focus lies at a higher point, for instance in the apical cell itself. The figures of Schwendener clearly demonstrate that this is actually the case in the Marattiaceae, in which the initial cells appear almost oblong in longitudinal section. Lastly, it is clear that in our second type the four initial cells may be represented to the mind as being gaps in the system of construction in just the same sense as the idea is applied by Sachs to the single apical cell.

If now the observations above detailed for the roots of the Osmundaceae be compared with the two types of construction thus defined, it will be clearly seen that though subject to considerable variation of detail, they occupy an intermediate position between the two types: thus a single initial cell is but rarely found, the number being variable up to four, which seems to be the usual number for *Todea*; the sides of the

[1] Lectures, Engl. ed., p. 451.

initial cells are less inclined to one another than in the Polypodiaceae, etc., in which the construction is on the confocal type, and the initial cell or cells are thus deeper. Again, the apices of the cells are often truncate, the form of the initial cells being thus not pyramidal but oblong, as is the case in the coaxial type: in both these characters, which are, as above pointed out, to be connected with *a lowering of the centre of construction*, the roots of the Osmundaceae, and more especially of *Todea*, approach the Marattiaceous type.

While drawing this distinction between the two types of construction, and while recognising that the Marattiaceous type is consistently coaxial, it is to be remembered that a pure and consistent coaxial construction is exceptional and is found exemplified in the Marattiaceous type and in the Janczewski's fourth type of Angiospermic roots; the large majority of roots are mixed in the character of their meristem: thus in the leptosporangiate Ferns the construction of the root-cap is coaxial, while that of the body of the root is confocal: in the Gymnosperms the confocal character is limited to the plerome, while all the outer tissues are coaxial: in the Monocotyledons the whole is confocal with the exception of the root-cap. It has, however, been pointed out by Dr. G. Karsten [1] that in the development of certain individual roots there may be a transition from the coaxial type in the early stages, to the confocal in the older root: observations such as these show that too great importance should not he attached to these characters alone as defining natural affinities; but, on the other hand, if there be traceable in a series of forms a sequence of character of the meristems which follows the series as laid out on other grounds, the meristematic characters may well be used as strengthening the systematic conclusion; and this is the way in which such evidence is to be used in the Filicineous series [2].

From the comparative study of the meristems of roots of

[1] Ueber die Anlage seitlicher Organe. Leipzig, 1886, pp. 6–8.

[2] See conclusion of this paper.

the series of Filicineae the following conclusions may be drawn :—

(1) That the apices of roots of the leptosporangiate Ferns are of comparatively small bulk, while those of the Osmundaceae are more bulky, and those of the Marattiaceae still more so.

(2) That though the type of structure of the apex of the root in the leptosporangiate Ferns is stereotyped and regular, with one tetrahedral initial cell, in the Osmundaceae this regularity is lost, there being often three or even four initials.

(3) That the initial cells of Osmundaceae and Marattiaceae are narrower and deeper in proportion than in the leptosporangiate Ferns, and are often not pointed but rectangular at the base: this implies a lower position of the centre of construction.

(4) That in respect of the structure of the apex of the root the leptosporangiate Ferns, Osmundaceae, and Marattiaceae constitute a natural series, of which the first named are the simplest, and the last the most complex, while the Osmundaceae occupy an intermediate position [1].

Apices of Stems.

As regards the details of structure of the apex of the stem in leptosporangiate Ferns there has been some discrepancy of observation; but there is at least coincidence on this point, that there is present a single initial, or apical cell, the open question having been as to its *form*.

Hofmeister, in his 'Higher Cryptogamia,' [2] described a two-sided, wedge-shaped, apical cell for *Niphobolus chinensis* and *N. rupestris*, *Polypodium aureum* and *P. punctatum*, and for *Platycerium alcicorne*. He figures [3] two apices of *Polypodium vulgare*, which show that the actual form of the cell is variable, and an apex of *Pteris aquilina* in which it is of the form of

[1] For further details and figures relating to the roots of the Osmundaceae, reference may be made to my paper on this subject in Q. J. M. S. 1885.

[2] Ray. Soc. 1862, p. 248. [3] l. c., Plate XXXIV, Figs. 5, 6; text, p. 248.

a narrow, three-sided pyramid. Sachs[1] figures and describes the apical cell of this plant as a two-sided one, and summarises the knowledge acquired on this point thus :—'We may for the present take it to be the rule that creeping stems with bilateral structure have a two-sided apical cell, and that in erect or ascending stems with rosettes of leaves radiating in every direction, the apical cell is a three-sided pyramid.' But the wide observations on the apices of dorsiventral Ferns by Dr. L. Klein[2] clearly disproved this generalisation: he investigated fifty species, belonging to nineteen genera, with the result that, excepting *Pteris aquilina*, all had a three-sided initial cell at the apex of the stem: further, Klein found that the form of the apical cell is variable in *Pteris* itself. Even in *Ceratopteris*, with its thin and elongated apex, a three-sided initial cell is present[3], though it might have been anticipated that in so slender a form the construction might have been simpler: the stem however is upright, and the leaf-arrangement spiral. Passing to the Hydropterideae, in *Azolla*[4], and in *Salvinia*[5], the apex of the rhizome has been shown to be occupied by a two-sided cell, with segments alternating on opposite sides; in *Marsilia* however[6] there is a three-sided cell: the same appears to be also the case in *Pilularia*, according to my own observations, and Campbell[7] appears to have come to the same conclusion, for though he does not state the fact directly, he allows it to be inferred, since he speaks of a 'third or ventral segment': there is in fact a difference in the structure of the apex of the stem between the two sections of the Heterosporous Filicineae, the more distinctly aquatic forms being the simpler. Thus observations on a large number of leptosporangiate Ferns have shown that whether the stems be dorsiventral and creeping, or radial and erect, the apex is occupied by a three-sided pyra-

[1] Textbook, 4th German edition, p. 423.
[2] Bot. Zeit., 1884, p. 577.
[3] Kny, Parkeriaceae, p. 28.
[4] Strasburger, Ueber *Azolla*, p. 17.
[5] Pringsheim's Jahrbücher, IV.
[6] Hanstein in Pringh. Jahrb. IV, Taf. XIV, Figs. 4, 5.
[7] Annals of Botany, II, p. 260.

midal apical cell; but that this rule is not without exceptions among dorsiventral forms, such as *Pteris aquilina*, *Azolla*, and *Salvinia*, in which a two-sided cell is present.

On various grounds it had seemed to me not improbable that the dorsiventral axes of the Hymenophyllaceae might also prove to be exceptions, and have the simpler construction of the apex: these have, as far as I am aware, never hitherto been thoroughly examined on this point[1]: it is true that Prantl[2] has made some observations on *Trichomanes speciosum* and *T. pyxidiferum*, but he admits that they were insufficient owing to lack of suitable material. Having had access to the fine collection of living specimens in the Royal Gardens, Kew, observations have been made on several of the more robust species of Hymenophyllaceae, in which the difficulties of manipulation are less than in the minute forms, and the security of the observations accordingly greater. The result is constantly to find the apex occupied by a three-sided pyramidal initial cell.

In *Trichomanes radicans* the rhizome is rather bulky, and its apex flat (Fig. 18): upon this rhizome the leaves arise alternately on opposite sides. Seen in surface view (Fig. 19) the apex is occupied by a three-sided cell, of which one side is directed downwards, and one edge upwards. The segments, which are cut off from the successive sides, are relatively bulky, and from the appearance of the whole meristem it would appear that the growth of the segments is much more rapid than that of the apical cell itself. Only a small proportion of the segments take part in the formation of the leaves, and I have been unable to recognise any numerical relation between the segments and the leaves formed. The latter arise from that part of the upper or dorsal segments which adjoins the ventral or lower segments (Fig. 19 *b*). In the axil of each leaf arises an axillary bud, which is constantly present, and may therefore be styled a 'stable bud' in the sense of Strasburger[3].

[1] No species of Hymenophyllaceae were examined by Klein.

[2] Hymenophyllaceae, p. 26; Plate I, Figs. 6, 7, 9.

[3] Azolla, p. 22.

Longitudinal sections show that the apical cell, both of the main axis (Fig. 20) and of the axillary bud (Fig. 21), is pointed and rather deep: deeper in fact than is usual with the apical cells of the stems of most leptosporangiate Ferns; this is however to be put in relation with the flattened form of the apex, and Prantl's figures[1] seem to indicate that it is not so in the slender forms.

The rhizomes of the following species were also examined; viz. *Trichomanes reniforme*, and *Hymenophyllum caudiculatatum* and *demissum*: in each a three-sided pyramidal apical cell was found, but in the two last-named species the further subdivision of the segments was found to be less regular than in *Tr. reniforme* or *radicans*. From these observations it appears that the rhizome of the Hymenophyllaceae corresponds, as regards the essential characters of its apex, to the structure of the apex of the stem in the large majority of other leptosporangiate Ferns.

On the apex of the stem of other leptosporangiate Ferns I have little to add to the excellent observations of Klein. He seems, however, to have had little opportunity of examining the stems of Cytheaceae or Dicksonieae, and though he cites *Dicksonia rubiginosa* and *Hypoderris Brownii* in his list of plants employed, he does not figure either of them, or describe them in the text. As far as I am aware, no observations have hitherto been made on the structure of the apex of the stem of large and well-grown Tree-Ferns, and it would be reasonable to expect that the very large size of the stem might react upon the structure of its apex. Having collected, when in Ceylon, apical buds of large plants of *Amphicosmia* (*Hemitelia*) *Walkerae*, these were investigated with the following result: The apex of the stem is not very broad, and is slightly depressed, while the extreme apex rises from the hollow depression as a central cone: this is terminated by a large and extremely well-defined three-sided pyramidal apical cell, from the sides of which successive segments are cut off; these subdivide with considerable regularity, and the character of the whole is quite as

[1] l. c., Plate I, Figs. 6, 9.

definite and regular as in any of the Polypodiaceae (Fig. 22). Thus it appears that, notwithstanding the size and internal complexity of the mature stem, the character of the apex is essentially similar to that of the smaller forms.

I have but few facts to adduce as to the structure of the apex of the stem of the Schizaeaceae. Klein (l. c.) has investigated those of *Lygodium circinatum* and *scandens*, and appears to have found in them a structure similar to that of other dorsiventral Ferns, for he gives no special description of them[1]. I have examined apices of *Lygodium scandens*, and of *Aneimia hirta*, and they both conform to the ordinary type of structure with a three-sided apical cell, while the apical cone is comparatively flat.

Passing on now to *Osmunda regalis*, in a considerable number of well-grown plants, from Ireland and elsewhere, the apex of the upright stem was found to be terminated by a flat apical cone: the meristem is very thin-walled and watery, with greatly vacuolated protoplasm: in transverse sections, cleared with 'eau de Javelle,' in the majority of cases a three-sided apical cell is seen, from which segments are cut off in the ordinary succession (Fig. 23); but the subdivision of the segments often shows irregularities. The size of the segments relatively to that of the initial cell is variable in different cases, and this will be recognised on comparing Figs. 23, 24. In some cases the form of the cell is not regular: thus in Fig. 24 it is four-sided, and the succession of segments is not so readily to be traced as in Fig. 23. In some few apices which were observed it appeared to be impossible to refer all the tissues to any one initial cell (Fig. 25). Now it is to be noted that all these figures were drawn from sections which included the outer wall of the cells: they represent with accuracy what is seen on viewing the apex from above, and no allowance need be made for distortion of the cells in preparation. Taking then Fig. 25 as representing accurately the actual arrangement of the cells, it seems probable that more than one initial is present, but the structure is such as cannot readily be referred

[1] Bot. Zeit. 1884, p. 647.

to any one of the ordinary types of construction. Here we have one of those strangely irregular arrangements analogous to those which have already been observed in the root, and a comparison of this with the apices of stems of the Marattiaceae described below will show the same similarity to the latter as has been traced in the root. It is to be noted however that the large majority of apices of the stems of *Osmunda* conform to the ordinary leptosporangiate type, and such examples as that shown in Fig. 25 are the exception rather than the rule.

The meristem being thus at times irregular, as seen in surface view, and the subdivision of the segments being variable, it is to be expected that the study of it in longitudinal section would present difficulties, and I have not been able to trace any definite and characteristic mode of segmentation. Longitudinal sections cut from a considerable number of stems show that a conical apical cell is usually present (Fig. 26), which is rather deep in proportion to its height: the relations of the surrounding tissues, and their reference to regularly succeeding segments are difficult to recognise. Thus it is seen both from transverse and longitudinal sections that, though the presence of a single initial cell may be ascertained in most cases in the stem of *Osmunda*, it is not always present, and the apical meristem is of a less regular and definite type than in the leptosporangiate Ferns.

Taking next into consideration the apex of the stem in the Marattiaceae, it may be noted that various accounts have from time to time been given of its structure[1]. Holle[2] ascribes to the apex of *Marattia* an elongated, four-sided apical cell: in *Angiopteris* he says that he cannot with certainty track the whole meristem as originating from a single initial cell, though he thinks that such an origin is probable.

Some years since I had the opportunity of examining the apex of one well-grown plant: a conical cell was recognised

[1] Hofmeister, Abhandl. d. K. Sächs. Ges. d. Wiss. 1857. Compare also De Vriese and Harting, Monogr. d. Maratt. pp. 49, 51. The papilla marked (*z*) which is there regarded as the apex of the stem, appears to be part of a young leaf.

[2] Bot. Zeit. 1876, p. 218.

in a median longitudinal section of this apex [1], which I took to be the single initial cell, but I was not able to state whether it had two or three edges, or what is the succession of segments cut off from it: further, the question was left open whether the presence of one initial is constant for the species, and the evidence was not considered as by any means conclusive. When in Ceylon, I took the opportunity of collecting apices of well-grown plants both of *Marattia fraxinea*, and of *Angiopteris evecta*, and though even this material has been too scanty for working out all the details of so complicated an apex as this has proved to be, still it has sufficed for acquiring some further knowledge of the meristems of this interesting family.

In large plants the apex of the stem is found to be almost perfectly flat, distinctly more so than in *Osmunda*: the very slightly swelling apical cone is unusually wide, and since the cells composing it are of almost equal size throughout, a careful examination of the tissue as seen in surface view is necessary before the succession of the cell-divisions can be traced. Treatment with 'eau de Javelle' was found useful for distinguishing the older or principal walls from the younger cell-walls, and thus assisting in the recognition of groups of cells of common origin. If a transverse section including the external surface of the apical cone of *Angiopteris* be thus treated, a central point may be recognised where the principal walls meet, and this point is often characterised by a highly refractive thickening of the wall: this is the central point of genesis of the meristem (Fig. 27): around this point are disposed cells which appear to be constant neither in number nor in form: it is true that the four cells marked (*) in Fig. 27 can be regarded as initial cells for the whole meristem, and it is possible to recognise how in this case the whole of the broad area of tissue represented might have been derived from them, the apical structure being thus coincident with that described by Schwendener for the root; but it is to be observed that this was the most favourable and distinct specimen of the

[1] Phil. Trans. 1884, Part II, Plate 37, Fig. 9.

whole number which I had under observation. Accordingly I am not prepared to state that the structure of the apex of the stem always accords to the type of Schwendener, though in some cases it undoubtedly appears to do so: it is possible that Holle's observations having been made on young plants (l. c. p. 216), their apices may have had a more simple structure with a single apical cell, such as he describes.

The apices of several strong stems of *Marattia fraxinea* were also examined, and the results are virtually the same as those for *Angiopteris evecta*; no single initial cell has been found; the meristem is however referable, in some cases at least, to four or five initial cells (Fig. 28), but these are not exactly alike in size or in shape. Whatever the details of the construction may be, there is obviously no single initial cell of definite shape, such as is found in the lower forms.

The study of longitudinal sections through the apex presents greater difficulties, as is always the case where the segmentation is not according to a definite scheme: it is essential at once to recognise that the conical form does not necessarily mark an initial cell, for in the first place undoubted initial cells may have a square base, as in the root of Marattiaceae or the rhizophore of *Selaginella*[1]; while conical cells are to be found at points where their character as initial cells is out of the question: thus in longitudinal sections through the leaf of *Angiopteris*, conical cells of considerable depth are to be found at points far removed from the actual apex. Naturally where the apex is very wide and flat, as it is in these plants, it is not easy to be certain which sections are median, and the uncertainty is increased where the character of the meristem is liable to variation: to the best of my belief the section shown in Fig. 29 is a median one; the wall (x,x) corresponds to that central point above recognised in transverse sections. It will be noted, first, that all the superficial cells of this region are unusually narrow and deep; thus, whatever the details of structure of the meristem,

[1] Treub, *Selaginella Martensii*, Plate IV.

the centre of construction must lie relatively low: also that two conical cells are present, one on either side of the wall (*x*,*x*); their position relatively to it is however not exactly alike. I am disposed to regard those two cells which are marked (*x*,*x*) as the initial cells, notwithstanding their difference in form, and the fact that their size is not greater than that of the surrounding cells. It is interesting at the same time to note the grouping of the cells; clearly the group to the right of the line (*x*,*x*) has been derived from a conical cell, which has undergone a T division, while the upper left-hand cell thus derived has divided irregularly to form, among others, the obliquely-based initial (*x*): the group to the left of the line (*x*,*x*) was apparently derived from a cell with a square base, and after somewhat irregular divisions this has resulted in the formation of a conical initial cell (*x*). These remarks, which are not presumed to give any exhaustive account of the structure of the meristem as seen in longitudinal section, serve at least to indicate this:—that longitudinal sections bear out the conclusions drawn from the study of the meristem in plan, viz. that in strongly grown plants there is no single initial cell at the apex of the stem of the Marattiaceae, and that the series of segmentations of those cells which are believed to be the initials is far from being regular.

I very much regret having to leave the investigation of the structure of these meristems in so unsatisfactory a position, neither being able to reduce the observations upon them to any strict system, nor being able to state directly that a definite system does not exist: such knowledge could only result from the examination of a very large number of specimens. But already my observations on the apex of the root of the Osmundaceae have shown that great irregularity and want of uniformity of construction are to be seen in them, and that irregularity which is found in the apex of the root of Osmundaceae seems to find its parallel in the apex of the stem of the Marattiaceae. But though it is at present impossible to demonstrate a strict type of segmentation for the apices of the stems of these plants, the following general conclusions

may be drawn from the comparative study of the apices of stems in the main series of Filicineae.

(1) That while the apex of the stem of most leptosporangiate Ferns is distinctly conical[1], that of the Osmundaceae and Marattiaceae is flatter, and more bulky.

(2) That, though in the leptosporangiate Ferns a single initial, with definite and regular segmentation, is always present, in *Osmunda* it is not always to be seen, while in well-grown plants of Marattiaceae a single initial is absent, the growth proceeding from a number (4?) of initial cells.

(3) That the initial cells of the Osmundaceae are narrower and deeper than is usual in leptosporangiate Ferns; in the Marattiaceae this is seen in a marked degree, and they are even to be found of rectangular form: these facts imply a lower position of the centre of construction of the meristem.

(4) That in the above respects the leptosporangiate Ferns, Osmundaceae and Marattiaceae, form a natural series, starting from those with a more convex form of the apical cone, and with simpler and more diagrammatic segmentation, and relatively high centre of construction, and proceeding to those with more complicated and less regular segmentation, and relatively deep-seated centre of construction.

(5) That these conclusions as drawn from the comparative study of the apices of stems correspond to the conclusions drawn from the study of the roots.

Apices of Leaves.

As we proceed upwards through the same series of Ferns as those above examined for the structure of the apex of root and stem, it will be seen that in the character of the apex of the leaf also a similar increase in complexity of the meristematic tissues is to be traced.

The observations of Kny[2], of Sadebeck[3], and of Prantl[4],

[1] *Trichomanes* seems to be exceptional in the flatness of its apical cone.

[2] Parkeriaceae, Taf. XXII–XXIV (=V–VII).

[3] Verh. d. bot. Ver. für d. Prov. Brandenburg, XV. 116.

[4] Hymenophyllaceae, pp. 4–7. Schizaeaceae, p. 3.

have laid the foundation of a knowledge of the mode of development of the fronds of Ferns: also in the Hydropterideae the development of the leaf has been carefully traced in *Marsilia*, *Salvinia*, and *Azolla*: I have also shown that the leaf of *Pilularia* originates in a manner similar to that of typical Ferns [1]. Notwithstanding all this there is still an open field for comparative observation on the mode of development of the leaf in different members of the Filicineous series: when it is remembered that the general character of the Fern plant is more closely dependent upon that of its leaves than on any other part, the omission to subject it to a more exact developmental study appears remarkable. The same mode of treatment will be applied here as in the root and stem: the leaf of the Hymenophyllaceae will be first considered, then successively those of other leptosporangiate Ferns, of Osmundaceae, and Marattiaceae. It will be assumed to be unnecessary to recapitulate the general results of other observers, and a reference to the writings above cited, and to the *précis* of the subject given by Sadebeck [2] will be sufficient.

Only very scanty facts are at present known as regards the origin of the frond of the Hymenophyllaceae, and for these we are chiefly indebted to Prantl [3], who has pointed out that in *Trichomanes speciosum* the leaf has a two-sided apical cell, and that from the segments a marginal series of cells is derived on either edge of the leaf. These points I have found to be correct for other species. I have observed early stages of development of the leaves in *Trichomanes radicans*, and find that they arise laterally upon and alternately on opposite sides of the axis: no exact numerical relation has been recognised between the leaves and the segments cut off from the apical cell of the stem, and it would appear that many segments pass without taking part in the formation of leaves. These arise from the lower edges of the obliquely lateral segments (Fig. 19 *l*), and appear as convex projections in

[1] Phil. Trans. Part II, 1884, p. 574. [2] Schenk's Handbuch, I, p. 270.
[3] Hymenophyllaceae, pp. 4–7.

which segmentation immediately proceeds so as to define a two-sided conical apical cell (Fig. 30); the position of this is such that one of its edges is directed towards the apical cell of the axis, the other away from it, and accordingly a longitudinal tangential section through the axis would, if it traversed a young leaf, show the conical apical cell of the young leaf, and the succession of its segments. I succeeded in obtaining such a preparation of a leaf in a very early stage (Fig. 31), and this shows that the apical cell is defined by the first cell-divisions after the convex projection of the young leaf beyond the surface of the axis; if a median section of the creeping rhizome be cut in a horizontal plane it would traverse the apical cell from edge to edge (Figs. 18, 32). When viewed from above, the segments are seen to be cut off from the apical cell in regular alternate succession (Fig. 30), and they are subsequently sub-divided by cutting off their adaxial and abaxial edges, so that the central part of each segment remains; this divides chiefly by walls parallel to the segmental walls, and the resulting cells are readily recognisable as the marginal cells (*m*, Fig. 30): it is important to note that this marginal series of cells, which plays so prominent a part in the ultimate conformation of the leaf in this as in other Ferns, is thus to be recognised as being initiated in the very first segments cut off from the apical cell; in other words, *the frond is here a typically winged structure to its extreme base.* It is also worthy of note that here, as in most leptosporangiate Ferns, the external area of the segments is relatively small as compared with the apical cell, while in the higher members of the series, if an apical cell be present, the segments appear relatively large (see page 335).

The young frond which thus originates, soon assumes the circinate curvature; it may even be seen in Fig. 30 that the growth is less active on the adaxial than on the abaxial side; but the curvature is very clearly seen in longitudinal sections (Fig. 32), which also demonstrate that cell-division is more active on the convex side, accompanied by occasional forma-

tion of conical cells (*o*). On the circinate phyllopodium [1] thus formed, which has a marginal series of cells continuous on either side to its extreme base, the pinnae begin to make their appearance as monopodial branches, ranged on the lateral flanges or wings which grow out from the marginal series of cells; the first-formed pinnae originate distinctly below the apex of the phyllopodium (Fig. 32), and alternate on opposite sides of it; the marginal series of cells is continuous also over their margins, but no initial cell is to be seen at their apices. On the other hand, the apex of the phyllopodium may be seen to have a clearly defined apical cell, even after a considerable number of pinnae have been formed, and this in itself would preclude the idea of a dichotomous branching; Prantl [2] has described the branching of the leaves of the Hymenophyllaceae as 'purely dichotomous'; this is certainly not the case for *Trichomanes radicans*.

I have also made observations as to the persistence of the apical cell of the phyllopodium, a point which Prantl left undecided from want of suitable material. In a leaf which had already formed sixteen pinnae the apical cell was still clearly recognised, while in leaves respectively with twenty-three and with thirty-two pinnae no apical cell could be seen. It is probable that there is no strict time when its identity is lost, but that ultimately it undergoes a T division [3] (which I was fortunate enough actually to observe in *Trichomanes reniforme*, Fig. 33), and so passes over into the marginal series [4]. It may be added that the monopodial type of branching occurs not only in the phyllopodium, but also in the pinnae, and in one case it was clearly recognised that the eighth pinnule originated in a monopodial manner, distinctly below the extreme apex of the pinna. Subsequently, however, both in the phyllopodium and in the pinna the

[1] This term has been adopted for the rachis or main axis of the leaf, whether branched or not. Phil. Trans. 1884, II, p. 569.

[2] l. c. p. 14.

[3] Compare Sadebeck, Entw. u. Wachsthum d. Farnblattes, p. 10, and Fig. 6.

[4] It is not inconsistent to regard the apical cell itself merely as a special cell of the marginal series.

mode of branching passes over by imperceptible gradations from the monopodial to the dichotomous, the branchings approaching successively nearer and nearer to the extreme apex. It is thus to be clearly understood that, though in *Trichomanes radicans* the ultimate branchings of the frond are of the dichotomous type, the earlier branchings are monopodial, and that the transition is to be seen in the individual frond, as is the case in other leptosporangiate Ferns. Further, though no sharp limit can be drawn between the two, it is to be noted that the monopodial branching is characteristic of that part of the frond where a wedge-shaped apical cell is present, while the dichotomous branching is characteristic rather of that part where T division is found at the extreme apex; the pinnae, however, which have at no time a wedge-shaped apical cell, branch monopodially in their lower parts: the state of matters in *Trichomanes radicans* seems accordingly to be this:—(1) that dichotomous branching occurs only where T division is found at the apex; (2) that where a wedge-shaped apical cell is present only monopodial branching takes place.

The mode of development of the wings will be described later (see p. 342).

Observations were also made on *Trichomanes reniforme*, as being a most markedly different species as regards the character of the leaf: here as before a wedge-shaped apical cell, and marginal series were found, but the identity of the apical cell is lost at a comparatively early period, by the appearance in it of a T division (Fig. 33); since there are no pinnae formed in this species it is difficult to draw a comparison between the period when this division takes place and the disappearance of the apical cell in *Trichomanes radicans*.

Such observations as I have made on *Hymenophyllum Tunbridgense* fall in with those on *Trichomanes*, and putting these together with the observations of Prantl, it may be concluded that a two-sided wedge-shaped apical cell is constantly present at the apex of the young leaf of the Hymenophyllaceae, and that a series of cells derived in the

first instance from the central portion of each segment, occupies the entire margin of the phyllopodium, pinnae, and pinnules.

Such observations as have been made on the development and apex of the leaves of Ferns have been chiefly on the Polypodiaceae; in face of the precise descriptions of Sadebeck [1], Klein [2], Luerssen [3], etc., it seems unnecessary to go further than recapitulate the general conclusion that the apex of the leaf is at first occupied by a two-sided wedge-shaped apical cell, from which segments are cut off alternately on opposite sides; that the central part of each segment contributes to the marginal series of cells, which is continuous up to the apex, and over the apex after the identity of the apical cell is lost: thus in most points there is similarity in the apical meristem to that of the Hymenophyllaceae, though the resulting frond is as a rule more robust. Klein mentions and figures [4] certain exceptional arrangements of the segmentations in young leaves of the Polypodiaceae. He points out that the apical cell is not always from the first a regular two-sided one, but that sometimes, the second wall only meeting the first on one side, a *three-sided initial* is temporarily present; this form may in some cases be maintained for a considerable time [5], but always passes over ultimately into the two-sided form. We shall see that this condition, which is only temporary and exceptional in the Polypodiaceae, becomes typical in the Osmundaceae, in which a three-sided initial is constantly present.

Observations were also made on the origin and apex of the leaves of *Amphicosmia* (*Hemitelea*) *Walkerae*, Hk., and it was found that the leaves originate laterally on the apex, in almost simultaneous whorls of three, the successive whorls alternating with one another. The first appearance of the leaf is just as in other leptosporangiate Ferns, by outgrowth of a single superficial cell, which becomes convex, and is

[1] Schenk's Handbuch, I, p. 270. [2] Bot. Zeit. 1884, p. 585, etc.
[3] Handbuch der Syst. Bot. I, p. 511.
[4] l. c. p. 486, and Figs. 2, 7, 21, 23, 26, 36. [5] l. c. Figs. 11, 22.

divided by alternate walls so as to define at once a two-sided, wedge-shaped apical cell, one edge of which is directed towards the apex of the stem; this apical structure is maintained for a considerable time: thus in its segmentation and the general characters of the apex there is nothing specially worthy of note in *Amphicosmia* as differing from other leptosporangiate Ferns.

For purposes of comparison a few observations have been made on *Lygodium scandens*, and *Aneimia hirta*, with the result that in both the apex of the leaf was seen to be occupied by a two-sided apical cell, from which segments, and a marginal series are derived as usual: in fact, as regards the early development of the leaf they show no advance on the Polypodiaceae. Thus it appears that in the leptosporangiate Ferns there is great uniformity in the segmentation of the young leaf, the only exceptions to the two-sided apical cell hitherto observed among them being those abnormal cases noted by Klein: the type of construction of the apex is that characteristic of flattened growths.

I have already drawn attention to the fact[1] that in the Osmundaceae there is a departure from the more simple type of structure of the apex of the leaf above referred to as characteristic of the Hymenophyllaceae, Polypodiaceae, Hydropterideae, Cyatheaceae, and Schizaeaceae: it has been pointed out that the three-sided type of apical cell which Klein showed to be occasionally found in very young leaves of the Polypodiaceae, is the type for *Osmunda* and *Todea*, though the succession and form of the segments in these plants is much more regular than that shown in Klein's figures. I have recently made fresh observations on *Osmunda regalis*, with the following results. The position of the apical cell which is defined by the first divisions in the young leaf (Fig. 23, *l*), is such that one of the sides faces the apex of the stem, while the opposite angle is directed away from it; this orientation seems to be constant for *O. regalis* and *cinnamomea*, and for *Todea superba*. The sub-division of the

[1] Phil. Trans. 1884, Part II, p. 575.

segments is far from being constant, a fact which has been noted and figured in my former paper (l.c. Fig. 7): it is shown obviously in Fig. 34, in which each segment divides by a sextant wall (*s,s*) into two approximately equal halves, but their further sub-division cannot be reduced to any rule, the resulting cells being triangular, or variously polygonal as seen in surface view from without. Longitudinal sections of the apex show that the apical cell is pointed, and deep in proportion to its width (Fig. 35), in fact very much deeper than the apical cells of the leptosporangiate Ferns[1]; in all the Ferns quoted in the foot-note the apical cell of the leaf is proportionately much less deep than it is in *Osmunda*: in other words, the centre of construction in *Osmunda* is more deeply seated than in any of these Ferns, and, coupling this with the more complicated construction of the meristem, which is of a type characteristic of cylindrical rather than flattened structures, the conclusion is that the whole member is of a more robust order than in other leptosporangiate Ferns.

It is obvious from an inspection of apices shown in plan (Fig. 34, also Phil. Trans. 1884, Plate 37, Figs. 4, 6, and 7), that here there can be no marginal series of cells having such relation to the segments of the apical cell on the one hand, and to the wings on the other, as in the leaves of the simpler type; and I have already shown in the paper above quoted, that each of the lateral wings is formed from parts of two of the rows of segments cut off from the apical cell. The structure of the wings will be described later (p. 352). It may further be added that, as far as my observations go, the branching of the frond of *Osmunda* is exclusively monopodial.

It will now be shown that in the Marattiaceae the divergence of the apex of the leaf from the type of the simpler Ferns, as regards the structure of the apical meristem, is even

[1] Compare Fig. 31 above: also Sadebeck's Fig. 33 C. (Schenk's Handbuch, I. p. 271) of *Asplenium Trichomanes*: also Hofmeister, Fig. 2, Plate XXXII. in his Higher Cryptogamia, which is drawn from *Pteris aquilina*: also the beautiful drawings of Kny on Plate XXIV. of his Memoir on *Ceratopteris*: also Prantl's figure of *Aneimia* (Schizaeaceae, Plate III, Fig. 28 B).

more marked than in the Osmundaceae. Holle[1] has investigated the apex of the leaf of the Marattiaceae; but it is not clear from his description whether his observations refer to *Marattia* or to *Angiopteris*, or to both genera. He finds the flattened apex of the leaf to be occupied by a single wedge-shaped apical cell, which is neither two nor three-sided, but of irregular section, and from it segments are cut off without regular order: he states that the identity of the apical cell is maintained till after the origination of the pinnae.

An examination of numerous leaves of well-grown plants of *Marattia fraxinea* has led me to the following results:— When seen in plan, the apical meristem of a young leaf, as yet without pinnae, may show a single three-sided initial cell: from this segments are cut off in regular sequence (Fig. 36); it is, however, to be noted that, as in the case figured, the initial cell is of relatively small size, while the growth of its segments is relatively rapid: thus in Fig. 36, the fourth segment occupies nearly double the area of the other three segments and the apical cell together: comparing this with *Osmunda* (Fig. 34) the difference is obvious, for here the area occupied by the apical cell and the last three segments is distinctly greater than that of the fourth segment: a comparison of the apex of the leaf of *Trichomanes* (Fig. 30) also shows the area of the apical cell in proportion to its segments to be much greater. With this relatively more rapid growth of the segments than of the apical cell itself is associated (as in *Osmunda*) irregularity of sub-division of the segments: each divides, it is true, by a sextant wall into two halves, but the further sub-divisions follow no constant rule. Frequently they present an appearance as though a series of segments were cut off from one triangular cell, which thus acquires the aspect of an initial cell, and may be styled a 'secondary initial': one such is seen in the abaxial half of the fourth segment in Fig. 36, and it will be subsequently shown that forms and arrangements of cells appear in longitudinal sections, which bear out the idea that these cells

[1] Bot. Zeit. 1876, p. 218.

assume in a secondary fashion, and for a short time, those qualities which mark the true initial cells.

But even in young leaves the apex does not always show such regularity as in this first case; thus in Fig. 37 the initial cell, though recognisable, is of less definite form; in Fig. 38 is seen the apex of a rather older leaf, and here the initial cell is still smaller, its segments less regular, and it is even difficult to see how the whole meristem can be referred as regards its origin to the one initial cell: secondary initials (*o*) are also present, but not in so marked a manner as in Fig. 36. Again, in a still older leaf, in which the pinnae were already formed, there was no single initial cell to be seen (Fig. 39): here the meristem has a structure resembling that of the apex of some of the roots of *Osmunda*[1]: three principal walls (*p*, *p*) are present, as in those roots, and the same theoretical interest attaches to that arrangement here as in the case of those roots: in fact, we may represent this condition to the mind as resulting from the continuation of the principal walls upwards, without deflection, so as to divide the apical cell itself, the result being, as in Fig. 39, that three initials would be produced (*x*, *x*); though 'secondary initials' are also present here, it is possible to refer the whole of this complicated meristem to three initials, each of which is formative of one-third of the meristem lying between two of the principal walls (*p*, *p*). The arrows in Figs. 36, 37, 38, indicate the direction of the apex of the stem, and a comparison will show that the orientation of the apical cell is not constant as in *Osmunda*, but that sometimes one side, sometimes one angle, is directed towards the apex of the stem.

The above results are borne out by a study of median longitudinal sections: in the young leaf of *Marattia* a single conical cell is found (Fig. 40), from which segments are cut off with considerable regularity; here and there other conical cells are found, which may correspond to the secondary initials above noted in plan: a prominent case of this is

[1] Compare Figs. 3 and 4.

shown in Fig. 41, in which the actual apical cell (*x*) is seen at the edge of the drawing, while from the conical cell (*o*) a succession of segments has been cut off. This would support the view that it is a secondary initial comparable to that shown in Fig. 7 of the root of *Osmunda*. Thus in the structure of the apex of the leaf of *Marattia fraxinea* there are many points in common with that of the Osmundaceae, but though a three-sided apical cell is present in the young leaf, neither in its size, form, orientation, or segmentation is it so regular as in the latter.

The apex of the leaf of *Angiopteris evecta* is more complex in structure than that of *Marattia*, and it may be stated at the outset that, though observations have been made on numerous leaves of various ages, including very young ones, no clear case of a single initial cell has been observed. This result falls in with the description given by me some years ago[1], that 'the cells of the apical region may be referred, in some cases at least, to a group of four initial cells; but these cannot always be equally well distinguished, and as seen in surface view from without they exceed the surrounding cells but little if at all in size.' I now find, on the basis of wider observation, that it is difficult to state the actual number of the initial cells, but the arrangement of the meristem seems in some cases to point to the number three: thus Figs. 42, 43, which show good typical examples, have been drawn as accurately as possible, so as to indicate the forms of the cells, and their genetic relations to one another: in neither case is it quite clear what the actual number of the initials is, but comparing these with one another, with Fig. 39 of *Marattia*, and again with Figs. 3 and 4 of the root of *Osmunda*, it would appear probable that we have here further examples of *three* initial cells (*x*) grouped together in the centre: thus it is possible, on theoretical grounds similar to those already explained in the case of the root, to put this more complicated construction of the apex in relation with the simpler type where one three-sided initial cell is

[1] Phil. Trans. 1884, Part II. p. 580.

present, such as is found sometimes in the leaf of *Marattia*, and constantly in *Osmunda*. It may further be noted that there is usually present a clearly defined longitudinal wall (*p*, *p* in the Figs. 42, 43), which runs at right angles to the median plane of the leaf: this divides the whole meristem unequally into adaxial and abaxial halves, and there appear to be as a rule two initials on the adaxial or posterior side of it, but only one on the abaxial or anterior side. Whether such cells as those marked (*o*) are actually initial cells for the whole of the areas indicated, or not (and such an arrangement has been seen in a number of leaves), I am not in a position to state definitely, but would point out that the arrangement of the cells about them is such as to lend countenance to such a view. Be this as it may, it is evident that the apex of this leaf is more complex than that of *Marattia*, and that there are at least three initial cells present. Inspection of these meristems as seen in plan also show that there is no marginal series of cells present here, having any such relation to the initial cells as that already noted in the leptosporangiate Ferns.

Longitudinal sections of so complex a meristem are naturally difficult of interpretation; the principal wall (*p*, *p*) is usually well marked, and cuts the meristem into anterior and posterior halves; this was recognised in my previous paper [1]. In a single median section (Fig. 44) several conical cells may be found, but, as already pointed out, the conical form does not necessarily imply that these are initial cells: even in sections which are believed to be exactly median it is very difficult to recognise the initial cells with certainty: the cells marked (*x*, *x*) in Figs. 44 and 45 are believed to be the initials, but I should not wish to state this point dogmatically. As regards the branching of the leaves of the Marattiaceae, it is exclusively monopodial, and on this point I have nothing to add to observations already published [2].

[1] l. c. p. 580, Fig. 12.

[2] l. c. p. 580, 586.

Comparison of Apices of Leaves.

If we pass in general review the characters of the apex of the leaf in the series of Ferns above described, as we proceed from the Hymenophyllaceae to the Marattiaceae, an advance in complexity of structure is to be seen similar to that already noted in root and stem; but it is even more marked here, since in the simpler forms the two-sided apical cell is constantly found. The following general conclusions result from a comparison of the apical meristems of leaves in the Filicineous series:—

(1) That the apex itself is more bulky, and its curvature necessarily less sharp in the Marattiaceae than in the Osmundaceae: while a similar relation holds between the Osmundaceae and the leptosporangiate Ferns.

(2) That in the leptosporangiate Ferns a two-sided apical cell with regular segments is the type for the leaf: that (as occasionally happens as an irregularity in young leaves of the Polypodiaceae) a three-sided apical cell, with three rows of segments is the rule for Osmundaceae: that in *Marattia* also this is often the case (though not always), but the growth of the segments is much greater in proportion to that of the apical cell than in *Osmunda*: that what is the exception in *Marattia* is the rule in *Angiopteris*, viz. that the apex is occupied not by one initial cell, but by a number, apparently three.

(3) That therefore, in respect of the structure of the apex of the leaf, the leptosporangiate Ferns, Osmundaceae and Marattiaceae form a natural and gradual series of which the first are the simplest and the last the most complex.

(4) That on rising through this series of Ferns the apical cells are proportionately narrower and deeper, while in the highest terms of the series the initial cells are often oblong with square base: thus there is a lowering of the centre of construction as we rise in the series.

(5) These results correspond to those already acquired

from a comparison of the apices of the root and the stem in the same series of plants.

The Development of the Wings of the Leaf.

The leaves of the large majority of Ferns are typically winged structures throughout their length: the wings are, however, variable in their devolopment; in the upper part of the leaf they are usually large and expanded, whereas in the lower part, they may be reduced in size, and only be recognised in the mature state as giving a slightly angular form to the transverse section, or merely as light-coloured and very slightly projecting longitudinal ridges: or they may widen out at the extreme base forming an almost sheath-like, or even stipular development. Though the mode of origin of the wings is known in some few forms, as far as I am aware their morphology and development have never been the subject of comparative study in the whole series of the Ferns, notwithstanding that they are so constant and marked a feature.

As with the stems and leaves of other vascular plants, so the leaves of the Ferns may develop either (1) in a simple cylindrical manner: this is very rare, but is seen in *Pilularia*; (2) as flattened, spathulate structures, without prominent wings or midrib, as in *Drymoglossum*; or (3) with an enlarged midrib, and thin, longitudinally-running wings on either side: this is the type for the very large majority of the Ferns. These wings may not only be traced down the phyllopodium, but may sometimes even be seen to be continuous to the stem itself: this is, however, the case only in Ferns with an elongated, creeping stem, as in *Pteris aquilina*, where they may be recognised as continuous light-brown lines, on either side of the rhizome, or in species of *Acrostichum* (*A. scandens*, Smith, and *A. tenuifolium*, Baker), in which case however they appear as discontinuous white streaks: with this may be compared such examples of winged stems among the Angiosperms as *Symphytum*, or *Vitis pterophora*.

On the leaf, when mature, the more or less largely developed wings may be traced upwards from the extreme base (e.g. various species of *Trichomanes*, *Aspidium*, *Pteris*, *Cyathea*, and in fact the majority of leptosporangiate Ferns), and along the whole margin of the frond, and extending over all the pinnae and pinnules; among the higher terms of the Filicineous series, however, this continuity, as seen in the mature state, appears at first sight to be broken, especially in the lower portions of the frond, where the phyllopodium often appears cylindrical (*Osmunda*, *Todea*, *Marattia*, and *Angiopteris*, etc.), there being only such slight traces of the winged character as those noted as occurring on certain rhizomes. Again, there are formed in connection with the wings, at the base of the leaves of some of the higher Ferns, sheath-like and 'stipular' growths (Osmundaceae, Marattiaceae): these also are more or less clearly continuous with the wings, and are to be regarded as the result of their peculiar development. That these basal growths, as well as those lateral lines, often discontinuous and but slightly marked, which are seen running up the leaf-stalk, are really metamorphosed wings, cannot be doubted, when it is seen that they may be traced upwards, and be seen to merge gradually into the typical wings of the upper portion of the leaf. Here also, as in the leaves of Angiosperms, a certain rough correlation is to be recognised: where the development, be it of leaf or axis, is robust, as a supporting organ, the wings are of a relatively reduced type: where the central phyllopodium is less bulky, there the wings are as a rule more largely developed.

The prevalence of wings on the leaves of Ferns is to be put in relation with what is known of the development: the leaf is a bilateral structure, and these wings are its margins: they are derived in the leptosporangiate Ferns from a marginal series of cells which is continuous over the apex, and thus at least in the simplest Ferns (the Hymenophyllaceae) the leaf is typically but one layer of cells in thickness at its apex: but immediately below the apex begins that thickening which

results in the midrib[1],—a structure which is necessary in order to strengthen and support the thin expansion: this formation of the midrib, which in the Hymenophyllaceae begins below the extreme apex, extends in the higher Ferns to the extreme tip; in other words, the leaf in early stages (Polypodiaceae), or throughout its whole length (Marattiaceae) may be of massive construction; but though this is the case, the wings which are borne laterally upon it are still to be recognised as corresponding to those of the Hymenophyllaceae, and represent the true margins of the bilateral leaf. On this ground, and also on account of the constant presence of the wings on the leaves of Ferns (and as far as I am aware *Pilularia* is the only case of their entire absence), they are parts worthy of more exact study than has yet been conceded to them. Since morphological importance of phenomena is measured chiefly by their constancy of occurrence in long series of organisms, these wings which are so constant and prominent in Ferns, as also in Cycads and many Angiosperms, must rank as parts which cannot be ignored. In studying the development of these wings, a similar series of forms to those above quoted in reference to the apices of root, stem, and leaf will be examined, and I shall show that, as we rise in the series, in point of structure of the young wing, an increase of complexity accompanied by a lowering of the centre of construction is to be traced, similar to that which has been demonstrated in the apices of root, stem, and leaf.

In describing the development of the leaf in the Hymenophyllaceae Prantl has already drawn attention to the early differentiation of marginal cells[2], and both he and Mettenius have figured and described the wings as consisting of a single layer of cells: this is typically the case for these plants, but as noted by both writers[3], it is by no means without exception, an increase in the number of layers being seen near the margin or near the nerves in various species, while in

[1] Compare Prantl, Hymenophyllaceae, Plate III, Figs. 38 A, B, C, and 39.
[2] Hymenophyllaceae, Plate I, Fig. 1.
[3] Mettenius, Hymenophyllaceae, pp. 457–8.

Hymenophyllum dilatatum, and *Trichomanes reniforme* the frond consists throughout of several layers of cells, but without stomata or intercellular spaces.

I have already pointed out that in the leaf of *Trichomanes radicans* a marginal series of cells is to be distinguished even from the very first segmentations (Fig. 30); that the segments divide so that comparatively small parts are cut off from their edges, while the middle part (*m*, *m*) goes to form the marginal series of cells: thus the leaf is from the very first a winged structure. If transverse sections be cut from the phyllopodium the wings will be seen on either side of it as thin projections, which are smaller below than higher up: whatever be the extent of their surface they appear to be never more than one layer of cells in thickness (Figs. 46, 47, 48). The marginal cells (*m*) retain their identity throughout, and are the cells from which all the others are ultimately derived: the segmentation of these cells is by transverse walls, and each of the marginal cells may, as regards its form and mode of segmentation when seen in section, be compared to the apical cell of certain Algae (e.g. *Chara*, *Polysiphonia*, etc.). An examination of the further developed wing shows that intercalary growth, in addition to the strictly marginal, takes place, as is indicated by division of cells at a distance from the margin (Fig. 48), but this intercalary growth is not specially localised. The development of the wings in the upper parts of the branched frond follow the same rule, and as regards the apices of the pinnae, etc., I can endorse the observations of Prantl on *T. speciosum*[1]. When seen in surface view the marginal cells of a young pinna are easily recognised, and their form is then seen to be that of half of a very narrow disc (Fig. 49). This form of the marginal cells, and simple mode of their segmentation by transverse walls seems to be the rule for the Hymenophyllaceae; it remained however to be seen whether those exceptionally thick-leaved forms above quoted would conform to the type: it is well known that the frond of *Trichomanes reniforme* is thicker than that of most other Hy-

[1] l. c. Plate III, Figs. 38, 39.

menophyllaceae, the reniform lamina being composed of four to six layers of cells, though it preserves the filmy character in as much as stomata and intercellular spaces are absent. Prantl conjectures shrewdly enough [1] that the origin of these many layers is by segmentation similar to that described by him for the origin of the nerves, but he had not the necessary material for proving this: the following statement will show that his conjecture was sound. It has been shown how the leaf of *Trichomanes reniforme* is provided with a marginal series of cells (Fig. 33); these give rise to the wings which run down the phyllopodium to its base: upwards the leaf widens out into the broadly reniform lamina. On cutting transverse sections of the lower part of the young leaf, the wings are seen as two round projections, in which the marginal cells do not undergo transverse segmentation, but the segments are cut off obliquely and alternately from opposite sides (Fig. 50): the number of segments thus produced is however small, and the wings of this part of the leaf are never largely developed. Now this mode of segmentation of the marginal cells is characteristic of the Polypodiaceae and other leptosporangiate Ferns, and is, to say the least, extremely rare in the Hymenophyllaceae: even here it is only seen near the base of the leaf, where, as in other Ferns, the structure of the wing is habitually more robust than in the upper parts [2].

Transverse sections of the reniform lamina of the mature frond of *Trichomanes reniforme* show that in the parts between the nerves it consists of four to six layers of cells, of which the central layers are larger and more watery, while the superficial cells have more protoplasm and chlorophyll: no intercellular spaces nor stomata are present. If transverse sections be cut from the young leaf a marginal cell of large size is seen in each, having a form similar to those found in the thin frond of *Trichomanes radicans*, etc. (Fig. 51) [3]:

[1] l. c. p. 23.

[2] See below, p. 350. Compare *Aspidium Filix-mas, Osmunda, Todea*, and *Marattiaceae*.

[3] Compare Fig. 47 of *Trichomanes radicans*, which is drawn to the same scale as Fig. 51.

from the half-disc-shaped marginal cells, successive segments are cut off by transverse walls, and these are subdivided in such a manner that the transverse section of the margin of the frond presents an almost identical appearance with that of a median longitudinal section through the apex of the midrib of other species[1]: thus Prantl's conjecture is correct, and though the ultimate bulk and complexity of the leaf in this species is as great as that in many of the Polypodiaceae, the marginal cells retain the form and simple segmentation characteristic of the Hymenophyllaceae.

The parallel case of *Hymenophyllum dilatatum* was also examined: exclusive of the nerves, the wings consist in this species of three to four layers of cells, usually three: of these the cells of the central layer are larger, while the superficial ones are relatively small. The wings extend over all the branches of the leaf, and may be traced down the petiole. In the young state a marginal series of half-disc-shaped cells is to be seen, from which successive segments are cut off by transverse walls, as in other Hymenophyllaceae (Fig. 52): the subdivision of these segments is singular, and seems to follow an almost regular rule: the segment first divides into two unequal parts (Fig. 52, the two youngest segments), by a periclinal wall, the larger cell then again divides, and the three resulting cells contribute to the three layers of which the mature wing is usually composed, and may undergo further divisions by anticlinal walls as in Fig. 54. When the marginal cell is about to cease its activity, irregular divisions appear in it, the walls being variously inclined (Figs. 52, 54), and the result is an appearance which at first sight resembles the segmentation of the marginal cells in the Polypodiaceae; but the same regularity does not hold here, and it is possible in all cases which I have observed to see (as in Figs. 53, 54) that these irregular and oblique segmentations succeed the more regular transverse ones: in fact they are not the type for this plant, any more than the oblique segmentation in the wing of

[1] Compare Prantl's Fig. 39, Plate III of *Trichomanes speciosum*: also Sachs' Lectures, Fig. 295 A.

Tr. reniforme towards the base of the leaf is for that species.

From the above descriptions it would appear that in the Hymenophyllaceae the wings extend from the base of the frond upwards over its whole margin, that (with the two exceptions above noted) the marginal cells have the form of half of a narrow disc: that segments are cut off from these by successive transverse (anticlinal) walls, and the fact that this mode of segmentation is retained, whether the expansions consist of but one layer of cells, or of more, is of special interest as showing that the arrangement of cell-walls is not entirely dependent on bulk, or on the external conformation of the part, but that there is a conservation of the type of segmentation in plants of natural affinity. Since the curvature of the segmental walls is very slight, while the walls by which the segments are further subdivided in *Tr. reniforme* and *H. dilatatum* cut them at right angles, it is clear that the centre of construction lies within the marginal cells themselves, and is situated comparatively near to the extreme margin of the wing.

Passing on now to the other leptosporangiate Ferns, in these, as in the Hymenophyllaceae, the leaf is habitually winged to its extreme base; but the wings of the lower part (petiole) are of a reduced type, and frequently appear there as mere longitudinal, light-coloured streaks. It is in Ferns of this class that the development and segmentation of the marginal series of cells is best known, and chiefly owing to the work of Kny and Sadebeck. It is generally known that a marginal series of cells is present, and that from them segments are cut off successively to form the flattened wings. On examining Kny's figure of *Ceratopteris*[1] it would appear that the segmentation of the marginal cells is similar to that in the Hymenophyllaceae, and this is made clear from a foot-note[2], in which this is stated to be the case. As far as I am aware, this, and in an obscure manner *Azolla*[3], and apparently also

[1] Kny, Parkeriaceae, Taf. XXIV, Fig. 7. [2] l. c. p. 40.

[3] Strasburger, Ueber *Azolla*, p. 38, Plate I, Fig. 20.

Salvinia, are the only examples among the leptosporangiate Ferns other than the Hymenophyllaceae, which constantly show this mode of segmentation, and it is to be noted that they are all aquatic forms. The prevalent type is that in which segments are cut off by walls obliquely inclined alternately to the upper and lower surfaces of the leaf: this has been described by various writers[1], but it will not, I think, be superfluous to add drawings illustrating the segmentation of the marginal cells, since the drawings hitherto published do not adequately represent the extreme regularity and beauty of segmentation which may be found in certain Ferns. If transverse sections be cut through the young pinna of *Pteris cretica*, and the structure of the young wing be examined, the whole of it will be seen to be referable in its origin to the marginal cell (Fig. 55): it is composed of segments cut off alternately by walls inclined to the lower and upper surfaces, the whole presenting an appearance such as that of a section through an apex with a conical apical cell[2]. In leaves which are unbranched the regularity of segmentation is less liable to be disturbed than in branched leaves: thus, if transverse sections be cut through the young leaf of *Scolopendrium vulgare*, the tissues may not only be seen in the young state to be referable in origin to the marginal cells (Fig. 56), but even when the wing has attained a very considerable size, the derivation of its tissues by segmentation from the marginal cells is still clear enough, and the segments, even to the number of sixteen, may be recognised in sections suitably cleared (Fig. 57). Referring to the segmentation of cells at the margins of flattened members, Prof. Sachs says[3]:—'A certain similarity of the cell network with that of a slender growing point with an apical cell impelled the earlier observers to assume in such cases a special type. They regarded cells lying beside one another at the margin as a series of neighbouring apical cells. This,

[1] Sadebeck, Entw. and Wachsth. des Farnblattes, Berlin, 1874; also Schenk's Handb. I. p. 270. Sachs' Lectures, Engl. ed. p. 459.

[2] Compare Sachs' Lectures, Fig. 295 B.

[3] Lectures, Engl. ed. p. 459.

from the purely formal point of view, is of course possible, but it contributes nothing further to the explanation of the processes of growth.' With regard to the wings of the leaves of Ferns, I cannot agree with this statement. If we accept the view that an apical or initial cell represents merely a break in the constructive system of the growing point, then the marginal cell (*m*) in Figs. 55, 56, 57 corresponds in this respect exactly to an initial cell of stem, leaf, or root, and just as from the latter (which may be one or more in number) by segmentation all the fresh tissues of the leaves of the member are derived, so also is all the fresh tissue of the wing derived ultimately by segmentation from the marginal cells: just as in the apices of stems, leaves, or roots, by tracing the origin and subdivisions of the segments we gain a knowledge of the manner of localisation of growth, so also may this be done in the wings. In fact, excepting the difference of form, number, and position, I fail to see that the initial cells of the apex of the stem, leaf, or root can with any reason be regarded in a different light from those initial or marginal cells which are found on the growing margin of the leaves of Ferns.

It is thus to be seen, both from the observations of others, and also from such examples as those above described, that in the leptosporangiate Ferns (exclusive of the Hymenophyllaceae) the type of segmentation of the marginal cells is more complicated than that of the Hymenophyllaceae; from each of the marginal cells two alternating rows of segments are cut off by oblique walls, while in the Hymenophyllaceae only one row of segments is derived from each marginal cell. As shown by a comparison of Sachs' diagrams[1] this latter type is associated with a deeper position of the centre of construction, and is thus characteristic of a more robust type of structure.

But among these Ferns the 'filmy' type of structure is not unknown, and I have had the opportunity of investigating the development of the leaf of *Asplenium resectum* in specimens from the Kew collection[2]. The leaf of this Fern is thin and

[1] Sachs' Lectures, Engl. ed. p. 457, Figs. 295 A and B.

[2] This Fern was brought under my notice by Mr. Staden, of the Royal Gardens, Kew.

pellucid, and examination of it when mature shows that stomata are absent from the thinner portions of the frond, which consist of but two layers of cells, with no intercellular spaces between them: thus it has the ordinary 'filmy' character. In view of the fact that *Trichomanes reniforme* retains that mode of segmentation of the marginal cells which is characteristic of the Hymenophyllaceae notwithstanding that its leaf is four to six layers of cells in thickness, it was a matter of some interest to ascertain what is the mode of segmentation of this 'filmy' *Asplenium*, and to see whether it would, notwithstanding its 'filmy' character, retain the segmentation characteristic of *Asplenium*[1], or show, in accordance with its texture when mature, the simpler type of segmentation of the Hymenophyllaceae. The result of the examination was to find that the segmentation is according to the more complicated type, two rows of cells being derived from each marginal cell (Fig. 58), and that these remain undivided by periclinal walls, except in the vicinity of the vascular bundles: thus its leaf represents the polypodiaceous type of segmentation reduced to its simplest terms. These observations lead towards the following conclusions:—(1) that the 'filmy' character may be assumed in Ferns of various affinity: this point will be discussed later; (2) that within the circle of affinity of the leptosporangiate Ferns the mode of segmentation is not dominated by the absolute size[2] or external conformation, but that there is in certain Ferns a conservation of that type of segmentation which is characteristic of the family to which they belong, irrespective of increase (*Trichomanes reniforme*), or decrease (*Asplenium resectum*) of bulk as compared with typical members of the same family.

But the type of segmentation with two rows of segments from each marginal cell is not constant throughout the whole length of the frond in the Polypodiaceae: just as in *Trichomanes reniforme* a more complicated structure is found in the

[1] Compare Sadebeck in Schenk's Handbuch, Vol. I. p. 271, Fig. 36 D.

[2] As regards absolute size compare Fig. 51 of *Trichomanes reniforme* with Fig. 58 of *Asplenium resectum*: they are both drawn to the same scale.

young wings towards the base of the leaf, so also here the structure of the wing at the base of the frond is more complicated than above. If transverse sections be cut from a young frond of *Scolopendrium* near to its base, the internal structure of the wings does not admit of their tissues being referred in origin to marginal cells similar to those typically found in the upper part of the leaf: they appear to correspond rather in structure and development to that more robust form to be presently described as typical for the Osmundaceae and Marattiaceae, in which no single series of marginal cells is present. Similar results are to be obtained from *Asplenium nidus*, *Aspidium Filix-mas*, etc.; in fact, it seems to be a common character among the Polypodiaceae that the wings are more bulky towards the base of the frond, and that their construction is there on a more complex type. There is thus, roughly speaking, a proportion between the greater bulk of the phyllopodium and that of the wings towards the base of the leaf, while both are less bulky and simpler in construction above. This corresponds to similar observations above noted in the leaf of *Trichomanes reniforme*.

Examination of the leaves of *Amphicosmia* (*Hemitelia*) *Walkerae*, Hk., shows that the type of the Polypodiaceae holds also for this representative of the Cyatheaceae. In the mature leaves of this plant the wings are but slightly indicated towards the base, appearing there as discontinuous longitudinal streaks, and in the young state a definite series of marginal cells is not to be recognised there; but transverse sections of the upper parts of the pinnae and pinnules show the marginal series of cells clearly defined, and with that regular alternate segmentation above described for the Polypodiaceae.

In connection with the 'filmy' development of Ferns an interesting question arises as to the nature of those strange growths called *Aphlebiae*, which are found attached to the base of the leaf of *Hemitelia* (*Alsophila*) *capensis*[1]: such

[1] I owe it to Prof. Bayley Balfour that my attention was drawn to this Fern, and it was on specimens supplied by him from the Edinburgh Botanic Garden

developments appear to have been frequent on the Ferns of earlier geological periods[1], though they are rare on living species. Dissection of the bases of the leaves of this plant shows that the profusely branched 'Aphlebiae' are inserted above the extreme base, and, like the normal pinnae, alternately along the marginal lines or wings: they vary in number, two, three, or four being found on each leaf: their branching is irregular at the base, but higher up they produce alternate branches of a higher order (pinnules), which are inserted on the reduced marginal wings. The higher branches widen out into thin, meagre expansions, which correspond in general conformation to the normal pinnae, but are of a much more reduced type.

Comparing their microscopic structure with that of the normal pinnae, it is seen that they show the same characters but on a reduced scale; e.g. the normal pinna is five layers of cells in thickness, the aphlebia only three to four; while stomata and intercellular spaces are present in both: thus the comparison of these aphlebiae to 'filmy' Ferns is based on slender grounds. All the facts above adduced point to the conclusion that the 'aphlebiae' of *Hemitelia capensis* are nothing more than peculiarly developed basal pinnae, and when the fact is added that on one of the Edinburgh plants a pinna was found showing intermediate characters between the normal and the aphlebiae, this conclusion is greatly strengthened. But what circumstances they are which have led to so strange a development of certain pinnae, and the question whether in all the cases in which such growths have been described for fossil forms a like explanation is possible, must remain for the present undecided.

Material could not be obtained for working the actual development of the aphlebiae.

From Prantl's account of the Schizaeaceae[2] it would appear

that these observations were made. Compare also Hofmeister, Higher Cryptogamia, notes on pp. 212, 243.

[1] Solms-Laubach, Palaeophytologie, p. 136.

[2] Schizaeaceae, p. 4. Compare his Plate VII., Figs. 109, 110, 111; Plate VIII, Fig. 133.

that the structure of the wings in these plants conforms, at least in the upper parts of the frond, to that of the Polypodiaceae. I have also noted that in *Aneimia* the wings of the basal part of the leaf are of the more bulky type: thus the Schizaeaceae appear, as regards the wings, to show no advance of complexity upon the Polypodiaceae.

Passing on now to the Osmundaceae, the structure of the young wings has been most exactly observed in *Todea barbara*, but observations have also been made on *Todea superba* and *T. hymenophylloides* (=*pellucida*), and on *Osmunda regalis*: it may be stated at once that (excluding the 'filmy' *Todeas*) the result is to find the wings in this family more complex than those of the true leptosporangiate Ferns.

Taking first *Osmunda regalis*, it has been stated by Kny[1] that marginal cells are present on the wings, from which, as in the Polypodiaceae, segments are cut off obliquely and alternately. This may be the case in young plants, but numerous sections which I have made from various parts of the leaf of this species fail to bear out the statement for well-grown plants: the construction of the young wing is found in old plants to be essentially similar to that to be described for *Todea barbara*; sometimes it is true that a series of larger cells may be seen from without to occupy the margin, while in section a wedge-shaped cell may be seen to lie at the extreme outer edge of the wing, but this is not constant, and when so found it is of relatively small size, while the segments never show that regularity of arrangement which is so characteristic of the Polypodiaceae. Knowing as we do that the apex of the leaf of *Osmunda* is occupied by a three-sided apical cell, and that the position of the wings corresponds to two of the angles of that cell[2], and that the edges of two rows of segments contribute to the formation of each wing, it would be contrary to all expectation that a definite marginal series should be found. In fact, I look upon the absence of

[1] Parkeriaceae, p. 40, footnote.

[2] Compare Phil. Trans., 1884, Plate 37, Figs. 4, 5, 6.

a definite marginal series as a very natural concomitant of the more complex construction of the apex of this leaf.

The base of the phyllopodium of Osmunda is considerably enlarged, so as to form a wide sheath, and the wings are here laterally extended: in the young leaf their margins are bluntly rounded, but later they run out into thin and membranous lateral flaps, consisting in part of but a single layer of cells: none the less are these to be recognised as developments of the wings, and a comparison may fairly be drawn between this thinning out of the wings, and that which is found in the upper parts of the leaves of *Todea superba* and *hymenophylloides*, and lends to them that 'filmy' character which will be discussed later. Above the sheath the phyllopodium of *Osmunda* is almost cylindrical, the wings being reduced (as in the petioles of the higher vascular plants), while in the upper part of the leaf, and especially the pinnae and pinnules, they are more extended. The leaf of *Osmunda* is thus winged throughout, but shows in its lower portion varieties of development which might be compared with such as are seen among the higher plants.

But it is in *Todea barbara* that the structure of the young wings, and the nature of the segmentations of the margins have been most carefully examined. I have already described the base of the leaf of *Todea superba*[1], and that of *T. barbara* is similar to it. In early stages of development the base of the leaf resembles that of *Osmunda*, being furnished with massive wings: later the activity of growth extends transversely across the face of the phyllopodium, resulting in such a development as may be compared to the axillary stipule which is not uncommon among Angiosperms, and also finds its homologue in the commissure of the Marattiaceae and in *Stangeria*. Here also the margins, which are at first blunt and rounded, extend as the leaf develops into membranous flaps, which consist at their extreme edge of only one layer of cells. The conformation of the upper parts is generally

[1] Phil. Trans., 1884, p. 578, Plate 37, Figs. 8 *a*, *b*, *c*.

similar to *Osmunda*, the wings being massive, and consisting of about nine layers of cells.

Now the question is how are these massive wings produced? If the margins of young wings be examined externally, no marginal series of cells is seen; they appear to be composed of a complicated net of relatively small cells, which are arranged more or less definitely in transverse rows (Fig. 59). Examining these rows individually[1] there is no single cell in each which can readily be fixed upon as a single initial for the whole row; in fact no marginal series of cells is present here, such as is found in the simpler Ferns. This conclusion is borne out by transverse sections through the young wing (Fig. 60), in which no single cell is obviously larger than the rest, and the segmentation is not by inclined and alternate walls, but there is a T division, the bases of the individual cells being not pointed, but approximately rectangular. It may frequently be seen, as in Fig. 60, that a clearly defined wall (x, x) divides the wing into two almost equal halves: in such a case the idea of a single marginal cell is clearly out of the question, and it appears probable that at least two initials are present in each transverse layer; if this were regularly the case the margin of the wing would be occupied by two longitudinal rows of initials placed side by side, which would take up the function performed in the leptosporangiate Ferns by a single row. It is clear enough that the origin of the tissues in Fig. 60 might be traced to the two cells marked (x, x): but though such a definite arrangement of the meristem may be found in some sections, it does not appear to be constant, nor does the surface view from without (Fig. 59) clearly point to such a conclusion. Accordingly, without actually defining the exact order of segmentation of the cells at the margin of the wing of *Todea barbara*, or even assuming that a fixed and definite rule exists, we may conclude (1) that no single series of initial cells is present; (2) that the superficial cells of the wing are of oblong form,

[1] It can hardly be doubted that these rows of cells correspond to one marginal cell together with its segments, in the Polypodiaceous type.

having rectangular bases; (3) that they undergo T division, and therefore (4) the whole segmentation of the wing is of a more complicated type than in the typical leptosporangiate Ferns: the whole wing is more massive, and the centre of construction more deeply seated.

These being the results of examination of *Todea barbara*, a peculiar interest attaches to the examination of similar points in the 'filmy' species of *Todea* (=*Leptopteris*, Presl.), and to the question whether the filmy character is to be taken as any indication of an affinity to the Hymenophyllaceae. I have already described the conformation of the base of the leaf of *Todea superba* [1], and in this respect, as also in the structure of its apex, it is essentially similar to the more robust *T. barbara*; but the pinnae and pinnules with their wings are more delicate: stomata and intercellular spaces are absent from the wings, which consist of but few layers of cells, and accordingly they have that delicate pellucid character which is described as 'filmy.'

The wings on the lower part of the phyllopodium are not largely developed, and appear when mature to be about three layers of cells in thickness: similarly, the wings of the mature pinnae and pinnules are three layers in thickness near to the midrib, but tail off towards the margin to a single layer: thus it is only at the margin that the wings actually attain the character of the simpler Hymenophyllaceae. As regards their development, *no marginal series is to be seen on any part of the leaf when young*; it is only subsequently that a rather irregular marginal series appears, and in their first segmentations the marginal cells follow the polypodiaceous type (Figs. 61, 62); but in some cases (Figs. 63, 64) the segmentation is rather that of wings of a more bulky character: later, however, as the wings grow more extended, they become thinner at the margin, and transverse segmentation such as is seen in the Hymenophyllaceae becomes the rule (Figs. 65, 66, 67); thus, as regards their development, these filmy wings of *Todea superba* show first, though imperfectly, the characters of the

[1] Phil. Trans. 1884, Part II, p. 578.

more robust Osmundaceae, and it is only as the filmy character becomes pronounced that the segmentation as in the Hymenophyllaceae appears. The points of most importance are (1) that no clearly marked series of marginal cells is present from the first; (2) that both the contour of the wing as seen in section, and its internal structure are variable; and (3) that though the segmentation is finally that seen in the *Hymenophyllaceae*, still where the whole structure when mature is but one layer of cells in thickness, no other mode of segmentation is possible but that by transverse walls.

Todea hymenophylloides (= *T. pellucida*) occupies an intermediate position between *T. barbara* and *T. superba* as regards the texture of the leaf: the thin expanded wings of the pinnae and pinnules have no stomata or intercellular spaces, and consist of three to four layers of cells, of which the superficial cells are relatively small, while the central are large, the margins do not run out to a thin edge as in *T. superba*: in fact, the structure of the wings resembles that of *Hymenophyllum dilatatum*, and accordingly the question of their mode of development is an interesting one for comparison. Transverse sections of the pinnules show that the wings do bear marginal cells, but that these are not large or prominent, nor is their segmentation very regular: in the large majority of sections the segments appear to be cut off alternately from the marginal cell, according to the polypodiaceous type, but the segments divide up according to no fixed rule (Figs. 68, 69): the cells which constitute the central layer are formed by periclinal walls, which apparently do not appear in all the segments. Thus it is seen that, though certain species of *Todea* assume in the wings of the upper parts of their leaves the 'filmy' structure which is characteristic especially of the Hymenophyllaceae, they do not at the same time assume the stereotyped mode of segmentation of marginal cells of the latter; and indeed a marginal series of cells seems not to be formed till a comparatively late period. When it is also remembered that the conformation of the base of the leaf and of its apical meristem corresponds to that of the robust *T. barbara*, the conclusion

naturally follows that the 'filmy' character is not a safe index of affinity, but that it is rather to be regarded as the result of adaptation. The general discussion of the filmy character in Ferns will be taken up later (page 378).

Passing on to *Angiopteris evecta* as a type of the Marattiaceae, the thick coriaceous wings may be traced in the mature leaf as extending, with varied development, over the upper part of the phyllopodium, pinnae, and pinnules: passing down the phyllopodium the wings become gradually reduced, till above the 'stipules' they are lost, and the base of the phyllopodium is almost perfectly cylindrical: at the base are the massive stipules, joined transversely by the fleshy commissure, and containing a well-developed system of vascular bundles. The development of these basal parts has already been described elsewhere[1], their first appearance being as a thick and massive weal, in which the component cells undergo repeated T divisions, and on comparative grounds it has been concluded that notwithstanding their size, massive character, and the presence of vascular bundles in them, they are to be regarded as peculiarly metamorphosed wings, and as comparable to the somewhat similar, though smaller growths in *Todea* and *Osmunda*[2]. It is well known that these stipules as they develop run out to a thin edge, which is almost transparent, with uneven margin, and consists at the extreme edge of but a single layer of cells; this we may I think rightly compare with the thinning out of the wings of the pinnae in *Todea hymenophylloides* and *superba*, and in this sense even the massive stipules of *Angiopteris* may be said to have 'filmy' margins.

The development of the wings of the pinnules was traced with

[1] Phil. Trans. 1884, Part II, p. 582; Plate 37, Figs. 10, 11.

[2] The presence of vascular bundles in the stipules of *Angiopteris*, while the corresponding outgrowths in *Todea* have none, need be no obstacle, since wings in different plants are very variable in this respect, e. g. bundles are absent in the wings of the pinnae of *Cycas*, while they are present in those of *Stangeria*. Again, the occurrence of vascular bundles is very irregular in the wings of the leaf of *Angiopteris* itself: it would appear rather that the presence of vascular bundles, here as in other parts of the shoot, depends roughly upon the area and bulk of the wings. In the stipular growths of *Stangeria* no vascular bundles are present.

the following results: the apex of the young pinnule appears rounded, so that transverse sections of it are circular, the formation of the wings not having begun; but lower down the wings appear as a rounded weal on either side: here (Fig. 70, *x*) the superficial cells increase in size, and are more densely filled with protoplasm than the rest: the projecting wing which thus originates does not spring from a single row of cells; the transverse section clearly shows that a number of cells take part in its initial formation, and these continue to grow and divide, while the rest of the pinnule, which finally constitutes the midrib, passes over into the quiescent condition. The cells forming the wing are of rectangular form (Fig. 70) and undergo repeated T divisions (Figs. 71, 72, 73); pyramidal cells are absent with the exception of those which form the hairs. As to the exact sequence of segmentation in the growing wing, I have not been able, any more than in *Todea barbara*, to recognise any invariable rule: sometimes (Figs. 71, 73) a group of cells, having obviously a common origin, occupy the centre of the transverse section, and in such cases it might be possible to recognise a certain cell as the permanent initial: in other cases (Fig. 72) the wing obviously originated from the outgrowth and repeated divisions of several cells, and the whole section of the wing may be seen to be composed of a number of groups of cells, each having apparently a distinct origin. I conclude that here, as in *Todea barbara*, though T division is the universal rule, there is no definite arrangement of the groups of cells composing each transverse section, so as to indicate their origin from any single initial. This mode of growth and segmentation of the wing is maintained throughout its development[1], the result being a massive structure of the wing, consisting of ten or more layers of cells.

The results of the above observations on the characters and mode of development of the wings of the leaves of Ferns may now be drawn together, and compared: the following are the chief points to be noted:—

[1] Phil. Trans. 1884, Part II, Plate 38, Fig. 19.

(1) That the leaves of the large majority of Ferns are winged, and that the wings may be traced, more or less distinctly, as continuous from the apex to the base of the leaf.

(2) That the wings are typically delicate and thin in the Hymenophyllaceae, that those of the Polypodiaceae are more robust, while in the Osmundaceae (excluding the filmy *Todeas*) and Marattiaceae the wings are thick and almost coriaceous.

(3) That the type of the Hymenophyllaceae is that each cell of the marginal series has the form of half a disc, and the segmentation is transverse (Fig. 47): in the Polypodiaceae the form of the marginal cell is a sector of a disc, and the segmentation is alternately from the upper and lower margins (Fig. 56): that in the Osmundaceae (excluding the filmy *Todeas*) and Marattiaceae there is no marginal series, but the cells forming the wing have square bases, and undergo a T division (Figs. 60, 72).

(4) That the Hymenophyllaceae, Polypodiaceae and other leptosporangiate Ferns, Osmundaceae, and Marattiaceae form a natural series as regards the complexity of structure of the young wing, the first-named being the simplest, and the last the most complex.

(5) That as we rise in this series, the centre of construction becomes more and more deeply seated, the progression in this respect being closely comparable to that above noted for the apical meristems of root, stem, and leaf.

(6) That in the Ferns observed (and it may be stated also for Ferns generally) the wing is of a more robust character near to the base of the frond than in its upper portions, there being thus some relation of bulk of the wing to that of the phyllopodium which bears it.

(7) That the wings may undergo various metamorphoses, being in some parts reduced, so as to be barely recognisable (petiole), in other parts being developed as broad flanges, or as the massive 'stipules.'

(8) That the 'filmy' character which depends upon thinness of the wings, and absence of stomata and intercellular spaces, is found to occur at three distinct points in the series, and

that filmy wings may be produced by various modes of marginal segmentation.

Sporangia.

Much more attention had been paid to the comparative investigation of the origin and development of the sporangia of Ferns, than to the other meristematic tissues, and I have but little to add to the facts already published elsewhere on this subject: nevertheless, in order to bring observations on the sporangia in line with the facts above detailed, and to show that the progress of other meristems from the simpler to the more complex as we pass along our series, runs parallel with a similar increase of complexity in the origin and construction of the sporangium, it will be necessary briefly to sketch out the characters of the young sporangium in the series of Ferns above cited.

On the ground of the mode of origination of the sporangium from a single superficial cell, or from a number of cells, Goebel has distinguished leptosporangiate from eusporangiate forms: and I shall show that this distinction, which divides a very natural series of plants, is in itself by no means a sharp line of demarcation. In drawing this distinction, however, Goebel has laid his finger upon a far-reaching difference of character, which finds its reflection in every meristematic tissue of the plants in question: in roots, stems, leaves, and wings, as well as in the sporangia, an increase of complexity of construction is to be seen as we pass upwards through the series of Ferns.

Without entering on details as to the exact succession of segmentations of the young sporangia, it will suffice for our present purpose to note that the sporangium of the Hymenophyllaceae[1], and Polypodiaceae[2], and other leptosporangiate Ferns arises typically as an outgrowth of a superficial cell. The first division in this cell is transverse in the Polypodiaceae[3],

[1] Prantl, l. c. p. 39: also Plate VI.
[2] Reess, Pringsh. Jahrb. v, p. 222. Kny, Parkeriaceae, p. 49.
[3] Reess, l. c. Plate XXI, Figs. 4, 5, 7.

dividing a basal or stalk cell from the cell which will form the head of the sporangium (compare diagram Fig. 88 *a*, *x*,*x*.): this I take to be the simplest segmentation of all. In the Hymenophyllaceae[1], in *Ceratopteris*[2], and in *Marsilia*[3] the first segmentation is frequently not transverse, but oblique, and this type I take to be nearer to the more complicated eusporangiate forms (compare diagram Fig. 88, *b*). This is, however, only a slight difference of detail; the main point is, that in all these Ferns the sporangium ultimately springs from a single superficial cell: in all of them it has been demonstrated by the writers above quoted that the position and order of succession of the divisions in the head of the sporangium show quite a diagrammatic regularity, and it will be remembered in connection with this that the structure of their apical meristems is comparatively simple and precise, a single apical cell with definite mode of segmentation being present; thus in these plants there is a parallelism between the structure of the apical meristems and that of the young sporangium.

It has been noted that in the Hymenophyllaceae the basal wall (*x*,*x*, diagram Fig. 88, *b*) is oblique: its position is apparently not quite uniform, but it appears usually to meet one of the lateral walls of the initial cell[4]; in the Schizaeaceae, however[5], this basal wall appears to be inserted actually on the periclinal (basal) wall of the initial cell (compare *x*,*x*, diagram Fig. 88, *c*), and is accordingly more inclined than in the previous cases. Though this may appear a trivial detail, it is to be noted as an indication of a lowering of the centre of construction of the sporangium, and of the assumption of a more robust and massive character. Though the sporangium of the Schizaeaceae is wholly derived from a single initial cell, it is, when mature, relatively large as compared with the other leptosporangiate Ferns, and it is seated on a short thick

[1] Prantl, l. c. Plate VI, Figs. 103–105, etc.
[2] Kny, Parkeriaceae, Plate XXV, Figs. 2, 3, 5.
[3] Russow, Vergl. Unters. Taf. VI, Figs. 62, 71, etc.
[4] Prantl, Hymenophyllaceae, p. 39, Taf. VI, Figs. 100, 104.
[5] Prantl, Schizaeaceae, p. 49.

stalk, and this character is foreshadowed by the first segmentations. In all the plants hitherto cited the wall of the sporangium consists of a single layer of cells, while a tapetum of not more than two layers intervenes between it and the spore-mother-cells.

Taking next the Osmundaceae, here as in the Schizaeaceae the sporangia are of relatively large size, and have short and thick stalks, and so they approach the Marattiaceae in these respects. The origin of the sporangium has been investigated by Prantl[1], and by Goebel[2]: the latter leaves the point still open whether or not the sporangium of *Osmunda* be referable in its origin to a single cell, as in the true leptosporangiate Ferns; and this is just one of those questions which, when dealing with transitional forms is so difficult to answer with certainty. If the origin be traced far enough back, doubtless the whole sporangium could be referred to a single cell, just as the whole plant may be ultimately referred in origin to the ovum; but without straining the point in such a way as that, it is often difficult to trace back the sporangium of *Osmunda* to a single cell, and in any case, a single initial cell does not project obviously outwards before segmentation, as is the case in the true leptosporangiate Ferns.

In *Osmunda regalis* the sporangia first appear as rather broad and very slightly convex projections on the wings of the pinnae and pinnules (Fig. 74); more than a single cell may take part, and though such cells often bear an obvious relation to one another, still it cannot be said in the same sense as in the leptosporangiate Ferns that the sporangium results from the outgrowth of a single superficial cell. In all cases, however, one cell distinctly takes the lead, and this we may call the initial cell (Fig. 75); but the arrangement of its division-walls does not, as in the true leptosporangiate Ferns, conform to any strict plan; the initial cells are oblong as seen in vertical section, and the first divisions are longitudinal, so as to meet the basal wall (Fig. 74): both in the segment thus cut off and in the central cell, periclinal, or sometimes oblique

[1] Bot. Zeit., 1877, p. 64.

[2] Schenk's Handbuch, III, p. 387.

divisions may take place (Fig. 75), so that a considerable bulk of tissue is formed, in the projecting apex of which a single large cell occupies a central position. This ultimately divides by a periclinal wall (Fig. 76), and the inner of the two resulting cells is the archesporium [1], which is completely surrounded by a single layer of other cells, and these, as in other Ferns, develop into the wall of the sporangium. The form of the archesporium is not definite and uniform as in other Ferns; and in most cases, instead of being pointed, its base is irregularly oblique; but the subsequent divisions, by which the layer of tapetal cells is cut off from it, follow with somewhat greater regularity (Figs. 77, 78), and the most common result is that the sporogenous cell (the true archesporium) has a tetrahedral form: nevertheless exceptions even to this are by no means uncommon (Figs. 79, 80). The whole sporangium, of which Fig. 77 may be taken as a good typical example, thus comes to consist of a short and massive stalk, a median longitudinal section of which shows four rows of cells; this bears the head, which is composed of a superficial layer which forms the wall of the sporangium, a tapetal layer, which is shaded obliquely in Fig. 77, and consists as yet of a single layer of cells. Towards the base of the sporangium, cells which have been cut off by extra oblique walls intervene between the tapetum and the superficial layer of the wall, giving the sporangium a more massive character than in the leptosporangiate Ferns (Figs. 77, 78, 80): there is thus a considerable bulk of internal tissue which takes no part in the formation of the spores (Figs. 81, 82). Subsequently anticlinal divisions appear in the cells forming the wall of the sporangium, but as no periclinals are formed the wall remains a single layer of cells in thickness even to the period of maturity; towards the base, however, it is supported internally by the cells above mentioned (Fig. 82). The tapetum divides

[1] I use the term archesporium for this cell before the tapetum is separated from it, because this is customary, and notwithstanding the inconsistency of so using the term, while in the higher plants it is applied to the cell from which the spore-mother-cells are directly derived.

first by anticlinal and later by periclinal walls, the result being two, or even three layers, the latter condition showing a greater complexity than in the leptosporangiate Ferns; but opposite the point where dehiscence takes place these divisions are delayed (*x*, Fig. 82). Meanwhile the sporogenous cell has grown, and divided repeatedly, and formed numerous spore-mother-cells, of which the number is much larger than in the Polypodiaceae; their number may be judged from the fact that more than twenty appear in a single section (Fig. 82). Each of these divides into four, the inner tapetal layer becomes glandular and disorganised, the outer however persists for a time, but dries up before maturity without becoming glandular.

I have already published a preliminary account of the origin of the sporangium in *Todea barbara*[1], and am now able to give a more full account with figures. This plant shows a structure and development of the sporangium which corresponds in all essential points to that of *Osmunda*, and there is a like irregularity as to the exact position and sequence of the segmentations. The essential parts of the sporangium appear to originate from a single cell with a square base, and deeply sunk in the tissue: having divided by a periclinal wall, the outer of the resulting cells undergoes anticlinal divisions (Fig. 83), by which three peripheral cells are cut off from a central cell (Figs. 84, 85): the whole group is still deeply sunk in the surrounding tissue, and the young sporangium projects as yet but slightly beyond the surface; it is clear from observation from without (Figs. 84, 85) that the disposition of the three lateral cells round the central one is similar to that in the Polypodiaceae, though the base of the central cell is often square. Then follows a periclinal division (Figs. 86, 87), by which the archesporium is cut off from a superficial cell: the form of the archesporium is variable, sometimes (Fig. 87) it is pointed below, and tetrahedral in form, as in the leptosporangiate Ferns; but this is the less common case: more frequently (Fig. 86) it has a square base; but even when this is so, the

[1] Q. J. M. S. Vol. XXV, p. 100, 1885.

subsequent divisions to form the tapetum may be inclined to one another, so that the sporogenous cell is ultimately tetrahedral, as in *Osmunda* (Fig. 77). In its further development the sporangium of *Todea* corresponds closely to that of *Osmunda* (compare the diagrammatic Figs. 88, *d*, *e*.).

Observations have also been made on the filmy Todeas (*T. superba*, and *T. hymenophylloides*): in both of these the sporangia are seated only on the more massive nerves, and do not arise from the filmy part of the pinnules. In these species the first stages of development were not noted, but sporangia were seen corresponding closely in structure to those of *Osmunda* (Fig. 77), and all observations I have made point to the conclusion that the development of the sporangium is in these species essentially similar to that in *Todea barbara*, or *Osmunda regalis*.

The mode of origin of the sporangium in the Marattiaceae is well known through the researches of various writers, but especially of Goebel[1]: for our present purpose the most notable points with regard to it are (1) that the sporangium is not directly referable in its origin to a single cell, i. e. it is eusporangiate; (2) that the archesporium is the hypodermal cell of the axile row of those cells which grow out to form the sporangium; (3) that it has a cubical form, and is deeply sunk in the tissue of the sporangium; (4) that the tapetum is derived from the cells surrounding the archesporium; (5) that the wall of the mature sporangium consists of more than a single layer of cells; and (6) that the sporangia which individually produce a relatively large number of spores, are massed together into bulky confluent sori (compare Figs. 88, *f*, *g*).

From a comparison of the characters of the young sporangia above noted, and of the diagrammatic figures (Figs. 88, *a–g*) which embody them, the following conclusions may be drawn:—

(1) That as regards the complication of the mode of origin, and the complexity of structure of their sporangia, the Hymenophyllaceae and Polypodiaceae, the Schizaeaceae, Osmun-

[1] Bot. Zeit., 1881, p. 681, etc.

daceae, and Marattiaceae form a natural series, the last named being the most complex.

(2) That in respect of reference of the sporangium to one or to more than one initial, the Osmundaceae are intermediate between the leptosporangiate and eusporangiate types, and that therefore this distinction cuts through a natural series of plants.

(3) That the increase of complexity is accompanied by a sinking of the centre of construction, similar to that already noted in the apices of root, stem, leaf, and wings of the leaf of the above series.

(4) That the change in form of the archespore (from the conical in the leptosporangiate Ferns to the cubical in the eusporangiate) is similar to the change of form of the initial cells of root, stem, leaf, and wing, observed as we rise in the above-named series.

(5) That the structure of the wall and tapetum is more complex in the eusporangiate Ferns, and the number of spores in each sporangium is larger, while the sporangia themselves are fewer.

(6) That no difference of importance in the sporangium is to be found between the filmy and the robust types of the Osmundaceae.

Conclusion.

A comparative study has now been made of each of those meristematic tissues which contribute to the formation of the sporophyte of the Fern, viz. of Root, Stem, Leaf, Wing, and Sporangium. Each of these has been examined in representatives of various divisions of the Filicineous series, viz. in the Hymenophyllaceae, Polypodiaceae, Cyatheaceae (in part), Schizaeaceae, Osmundaceae, and Marattiaceae. The main result is to demonstrate a singular parallelism in character of all the meristems in these several divisions, and to show that in the divisions first named the meristems are relatively simple in construction, and exhibit definite regularity of segmentation, one initial cell of definite form being present in

each[1]. Passing upwards through the series this simplicity and regularity is gradually departed from in each and all of these meristems; the structure becomes more complex, the identity of the single initial is lost, and the regular sequence of segmentations becomes less definite: this is associated in each case with a sinking of the centre of construction. The first-named divisions of the Filicineous series have a typically more delicate structure of their mature organs than those named later in the series, and this character comes out clearly also in the construction of the meristems. Taking into consideration for the moment the relative complexity of their meristems alone, the above list may be accepted as representing a natural series which graduates by gentle steps from the simpler to the more complex.

It may at first sight be felt that to use as a basis for arrangement of a series the detailed characters of the meristematic tissues, is to proceed on insufficient ground, and to approach too nearly to that cellular morphology which, if pursued universally and consistently into detail, would lead to unsound results; and those who are disposed to object will doubtless point out that there is not always a parallelism between all the meristematic tissues of a given plant. Thus in typically eusporangiate forms, such as *Ophioglossum* or *Equisetum*, a single initial cell with definite segmentation is found in stem and root: these exceptional cases will be again referred to below. In support of the main conclusion of this paper, however, it will be sufficient to point out that on the ground of comparative study of the external form and internal structure of both the sporophyte and the oophyte, the relative positions of certain families is already agreed upon: the main series of Ferns is recognised by recent writers as extending between two extreme types—the Hymenophyllaceae, which are considered to be of Algal-Bryophytic affinity,

[1] The results of the detailed examination *Onoclea Struthiopteris* by D. H. Campbell (The development of the Ostrich Fern; Mem. of the Boston Soc. of Nat. Hist. Vol. IV. No. II) fall in for the most part with those of other observers. I regret that this memoir only came to my hands after these pages had been set up in type.

and the Marattiaceae and Ophioglossaceae, which approach the Cycadaceae at least in the characters of the sporophyte. The evidence adduced in this paper is to be taken as materially strengthening this view, while it is also intended as a contribution to that knowledge which will be necessary for the final arrangement of the several sub-divisions of Ferns in sequence between these two extremes: thus the close relation of the meristems of the Osmundaceae, and especially of *Todea barbara* to the Marattiaceae, is clearly brought out. It is also seen that *Amphicosmia* (as an example of the Cyatheaceae), though so much larger than the ordinary Polypodiaceae, does not differ materially from them in the character of its meristems; and again, judging from the evidence adduced, the relation of the Schizaeaceae appears to be closer to the true leptosporangiate Ferns than to the Osmundaceae, notwithstanding that on various grounds they may be regarded as more nearly connected with the Osmundaceae than are the Polypodiaceae or Cyatheaceae.

As regards the sequence of the various groups of homosporous Ferns, various authors have arranged them in different ways—sometimes arbitrarily, sometimes with definite purpose. In the Synopsis Filicum [1] the order is :—

I. Gleicheniaceae.
II. Polypodiaceae [including Cyatheaceae and Hymenophyllaceae]
III. Osmundaceae.
IV. Schizaeaceae.
V. Marattiaceae.
VI. Ophioglossaceae.

Russow[2] speaks of the leptosporangiate Ferns as constituting six equivalent branches of the phylogenetic tree, and does not distinguish any one of them as specially approaching the Marattiaceae. Luerssen[3] gives the series thus :—

[1] Synopsis Filicum, Sir W. Hooker. [2] Vergl. Unters. 1872, pp. 194, etc.
[3] Handbuch d. syst. Botanik, 1879.

I. Hymenophyllaceae.
II. Cyatheaceae.
III. Polypodiaceae.
IV. Gleicheniaceae.
V. Schizaeaceae.
VI. Osmundaceae.
VII. Marattiaceae.
VIII. Ophioglossaceae.

This arrangement is also observed by Goebel[1]; though, oddly enough, the position of the Schizaeaceae and Osmundaceae is reversed where the special description of the groups is given (l. c. p. 228). This same reversed position is adopted also by Van Tieghem[2]; and from these facts I conclude that these authors had not recognised the near affinity of the Osmundaceae to the Marattiaceae. Prantl[3] suggests that the isosporous Ferns may be arranged, in respect of their general characters, in three groups, as follows :—

I.	II.	III.
Hymenophyllaceae.	Schizaeaceae.	Osmundaceae.
Polypodiaceae.	Gleicheniaceae.	Ophioglossaceae.
Cyatheaceae.	Parkeriaceae.	Marattiaceae.

He recognises the affinity more especially of the Schizaeaceae to the third group, and, on grounds which appear to me to be insufficient, especially to the Ophioglossaceae, rather than to the Osmundaceae or Marattiaceae.

It is thus seen that of the intermediate divisions of isosporous Ferns, the close relation of the Polypodiaceae and Cyatheaceae has been recognised by all the authors above quoted, and these two groups are placed by them next to the Hymenophyllaceae; this I believe to be their true position, and this conclusion is also borne out by the study of their meristems. The details of structure and development of the Gleicheniaceae are too imperfectly known to allow of their

[1] Outlines, p. 194, Engl. ed. [2] Traité de botanique, p. 1256.
[3] Schizaeaceae, 1881, p. 151.

position being definitely fixed at present: at the same time I may state that, as far as my observations on the meristems extend, they appear to correspond to the Polypodiaceae. The Schizaeaceae are recognised as those among the truly leptosporangiate Ferns which show affinities to the eusporangiate Ferns, while the Osmundaceae show that affinity much more distinctly, and most recent writers admit more or less fully that they form a connecting link between the leptosporangiate and eusporangiate members of the series.

But these conclusions, based chiefly upon the comparison of the sporophyte, are also borne out by the characters of the oophyte: thus the filamentous, protonema-like character of the oophyte of the Hymenophyllaceae is the simplest in structure of all the prothalli of Ferns, and indicates their relation to the Bryophyta [1]. The prothallus of the Polypodiaceae, after a short filamentous growth, widens out into the cordate expansion with circular 'cushion'; the Cyatheaceae resemble them in these respects [2]; the Schizaeaceae also appear to correspond to the Polypodiaceae in the characters of the prothallus [3], and this, as well as other grounds of comparison, lead me to conclude that their affinity to the true leptosporangiate Ferns is nearer than to the Osmundaceae. In the Osmundaceae the result of germination may be directly a massive prothallus, the filamentous stage being here lost [4]; often, however, the prothallus of these plants may first assume a flattened form. In the Marattiaceae the first result of germination may occasionally be a short filament, or more frequently a flattened expansion; but often the direct result is a massive body which, when the prothallus is mature, is thicker than that of the Osmundaceae [5]. Lastly, as far as it is known, the oophyte of the Ophioglossaceae is a solid, massive body. Though in comparison of the oophyte it is not

[1] See Bower, Annals of Botany, Vol. I, p. 270, where the most important literature on this subject is quoted.

[2] Bauke, Pringsh. Jahrb. Bd. X, pp. 49, etc.

[3] Sadebeck, in Schenk's Handbuch, I, p. 170.

[4] Luerssen, Zur Keimungsgeschichte der Osmundaceen.

[5] Jonkman, La Génération Séxuée des Marattiacées.

advisable to lay much stress upon details of conformation, the general progress of the oophyte in our series is shown to be from the filamentous type to that of a solid mass of tissue, that is, from the simpler type of construction to the more complex; and in this a parallel is seen to the observations above detailed on the meristems of the sporophyte in the same series. Again, if the antheridia and archegonia be compared in this same series, it will be seen that there is a progression in their mode of insertion. In the Hymenophyllaceae the antheridia are seated on stalks, which appear lateral or terminal on the filamentous oophyte [1], and the length of the stalk is often as great as the whole depth of the antheridium. In the other leptosporangiate Ferns the stalk, if present, is usually short, or the antheridium may even be sunk in the margin of the thallus [2]; in the Osmundaceae there is but little difference from these, but in the Marattiaceae and Ophioglossaceae the antheridium is deeply sunk in the tissue of the massive prothallus [3]. In the case of the archegonia also it is to be noted that in the Hymenophyllaceae the archegonia are exposed in groups on the relatively small archegoniophores and have projecting necks [4], while in the Marattiaceae [5] they are immersed in the tissue of the thallus and their necks project only slightly. Thus in the simpler terms of our series the sexual organs are exposed and project, while in the most complex forms they are protected by being sunk in the tissue of the oophyte.

Accordingly, whether the general character of the sporophyte or of the oophyte be considered, the divisions of the Filicineae would range themselves serially, according to their characters, in the same sequence as that indicated as the result of comparative study of their meristems; and since that is so, I think that no further answer is necessary to those who might at first feel an objection to the use of such apparently special

[1] Compare Annals of Botany, I, Plate XIV, Fig. 9; Plate XVI, Figs. 45–50.
[2] Kny, Monatsber. d. K. Acad. der Wiss. Berlin, 1869.
[3] Jonkman, l. c. Plate VII, Figs. 87–90.
[4] Annals of Botany, I, Plate XIV, Figs. 10, 16.
[5] Jonkman, l. c. Figs. 100–105.

characters as the details of meristematic structure as a ground for phylogenetic argument with respect to the series of Ferns.

We see then that on comparing a series of forms which on independent grounds marks itself off, and ranges itself in order as a natural series, there is in every one of the meristems of the plant to be recognised a progression, as we pass along the series, from the simpler to the more complex, from a definite type of meristem, characteristic of lower organised plants, such as Bryophyta and Algae, to a less definite and more complex type characteristic of higher organisation, such as that of the Gymnosperms and Angiosperms. It may with confidence be stated that at no point in the vegetable kingdom is such a transition so clear and so marked as in the Ferns. The significance of this transition is not far to seek: the lowest terms of our series, the Hymenophyllaceae, have probably a joint alliance to the Algae and Bryophyta, and are plants of characteristically semi-aquatic habit, living for the most part in air saturated with moisture, and in accordance with this habitat they have thin extended rhizomes, membranous fronds, thin roots, projecting sporangia, and a delicate usually filamentous prothallus with antheridia and archegonia freely exposed: here is seen in every part a relatively great exposure of surface in proportion to bulk, and accordingly, were it not for the wetness of the habitat, there would be danger of drying up on exposure to the air. Passing upwards along the series to the Marattiaceae, we see the transition by successive steps to plants capable of enduring without harm an exposure to considerable drought: we see, instead of the thin rhizome with scattered leaves, the thick upright stock with a terminal bud of leaves which protect its apex[1]; instead of the membranous frond, the thick, almost coriaceous leaf with massive wings; the roots instead of being thin become bulky: the sporangia do not project on a thin stalk, and so run the risk of drying up before maturity, but

[1] Here I speak in general terms: the majority (though not all) of the Hymenophyllaceae have creeping stems: the majority of the Marattiaceae have short, upright stems with crowded leaves; but species of *Danaea* are exceptions to this.

originate deeply in the tissue of the leaf, and are sessile and massive, or are even coherent together in masses when mature. Finally, in place of the filamentous, Alga-like oophyte, we find the fleshy and massive prothallus with its antheridia and archegonia not projecting and exposed, but protected from drying up by being sunk in the tissue. Every one of these characters points in the same direction: and if we once grant that the Hymenophyllaceae are phylogenetically the lowest members of the Filicineous series (a view which is held by all recent writers), then the Ferns illustrate in a most remarkable way the emergence of this branch of the Vascular Cryptogams from a semi-aquatic to a truly aerial habit. This is to me the real meaning of the lowering of the centre of construction, and consequent increase of robustness in all these meristems as we pass from the Hymenophyllaceae to the Marattiaceae: in it I believe that we see the expression of the fact that the higher plants of this series, by their more bulky habit, are the better adapted to an existence under circumstances of exposure to air which is not saturated with moisture. Regarding the series of green plants as a whole, those lowest in the scale are characteristically dependent upon water for their life, and especially for their fertilisation, and in this latter respect at least they betray their aquatic origin: in vascular plants it is seen that those which we regard as the higher in the scale are as a whole those best adapted to living in the air and in comparatively dry situations, and they are independent of external water as regards their fertilisation [1]. Among the Vascular Cryptogams, however, we see a series in a transition state, emerging from the semi-aquatic habit: the differentiation and construction of the vegetative organs of the sporophyte here shows a general similarity to that of the highest forms, but the sexual process, which is still dependent for its completion upon external water, is a clear index of their position lower in

[1] It is hardly necessary to point out that the aquatic Phanerogams are not typical Phanerogams, but that their simplicity of structure is to be regarded as a degradation: their fertilisation is, even in so extreme a case as *Vallisneria*, characteristically that of an aerial habit, i. e. siphonogamic.

the scale. Accordingly, while we rightly regard aquatic Phanerogams, which in many respects show similarities in detail of structure to the filmy Ferns, as exhibiting degeneration in accordance with their aquatic habit, I think that considering their position in the scale of Vascular Plants, we are justified in recognising the series of Ferns from the Hymenophyllaceae to the Marattiaceae, as an ascending series, and that this series illustrates the emergence of one phylum of the Vascular Cryptogams from the semi-aquatic to the aerial habit [1]: it is this which seems to me to give a special interest to the singular parallelism of characters of the meristems which I have demonstrated in this paper.

But in our series of Ferns the progressive adaptation of structure to external circumstances is especially to be recognised in the characters of the sporangia: in the Hymenophyllaceae these are aggregated in sori protected by a cup-like indusium from drying up while young, the youngest sporangia being nearest the base of the sorus, and accordingly most completely protected: in the Cyatheaceae the arrangement is similar, though the protection is somewhat less close and complete: in the Polypodiaceae the indusium serves as a protective cover during early stages: in all these Ferns the sporangia are stalked, and of small size, and each produces a limited number of spores, the sporangia being relatively numerous. In the Schizaeaceae the sporangia have shorter stalks and are of relatively larger size; they are not aggregated in so large numbers as in the Polypodiaceae, but (to judge from Prantl's figures [2]) this is compensated for by the larger number of the spore-mother-cells, and spores produced by the single sporangium. These characters become still more pronounced in the Osmundaceae:

[1] Obviously the converse view is capable of defence: it might be held that the Hymenophyllaceae owe their simple construction to their adaptation to a semi-aquatic habit, and that the Marattiaceae are the original type, from which the simpler Ferns have degenerated: general considerations of comparison of both generations, and of their position in the whole system lead me to think this view improbable.

[2] Schizaeaceae, Plate VIII, Figs. 120, 121.

here, the sporangia being of a still more bulky type, and massively but shortly stalked, the protection from evaporation from their surface when young is less necessary, and the indusium is no longer present: though the wall of the sporangium when mature is still only one layer of cells in thickness, it is more robust in early stages than in the proceeding types. I have pointed out (Figs. 77–78, 82) that extra oblique segmentations occur in the basal part of the sporangium, and that the tapetum may divide into more than two layers (Fig. 82), though this is the typical number for the simpler Ferns[1]. The number of spores produced from each sporangium is also very large[2]: thus the sporangia are relatively fewer, but more bulky and shorter stalked, and produce individually a larger number of spores: these are all characters leading towards the Marattiaceae. Finally, I have observed occasionally in *Todea barbara* a coalescence of two sporangia together. But this which is exceptional in the Osmundaceae is the rule in the Marattiaceae; not only are the sporangia sessile, large, and massive, with thick walls, and producing very numerous spores, but they are aggregated together in confluent masses, while an indusium is absent. These characters I regard as further indications of adaptation for protection against drying up while young, the lateral coalescence especially would well qualify the Marattiaceae for successfully developing their sporangia in exposed situations.

A comparison of these coalescent sori of the Marattiaceae, on the one hand with the sori of *Marsilia*, and on the other with the large and deeply sunk sporangia of *Ophioglossum*, led Strasburger[3] to conclude that the latter are not simple sporangia but 'sporocysts,' which, resulting from a coalescence of sporangia more complete than that of the Marattiaceae, really are, according to him, not homologous with the sporangia of the true Ferns, but with sori: this view he

[1] Compare Goebel's Fig. 103 D; Schenk's Handbuch, III, p. 388.

[2] Twenty-three spore-mother-cells are seen in the *section* shown in Fig. 82, while thirty are seen in section in Goebel's figure above quoted.

[3] Bot. Zeit. 1873, p. 84.

extends to the sporangia of *Equisetum* and to *Lycopodium*, and *Selaginella*, and it is still maintained by him in comparatively recent writings[1]. Now we have seen that the transition from leptosporangiate to eusporangiate forms is effected with the transitional step of the Osmundaceae within the Filicineous series, and without any lateral coalescence of simpler sporangia being necessary to bring it about; therefore, the eusporangiate sporangium is not in all cases a 'sporocyst.' To me the view that it ever is seems to be quite unnecessary and improbable: it is a much more simple interpretation of the deeply seated sporangia of *Ophioglossum* to regard each as a true sporangium, in which the shortening of the stalk, widening of the insertion, thickening of the wall, and increase in number of spores, are all carried to a still higher degree than in the Marattiaceae. To argue on such a point across from the Filicineae to the Lycopodineae and Equisetineae appears to me to proceed on the assumption of a much nearer relationship of these series than a comparison of their characters will justify: again, in their case I think that the view of their sporangia as coalescent 'sporocysts' is ill-founded.

On comparing the different vegetative members of the plant as seen in the series of Ferns, it will be found that as we rise in the series certain members retain the single initial more persistently than others. This will be seen from the following table, in which the numbers refer to the number of initial cells observed in each case:—

		Root.	Stem.	Leaf.
Hymenophyllaceae		1	1	1
Polypodiaceae, etc.		1	1	1
Schizaeaceae		1	1	1
Osmundaceae	(1) Osmunda	1–3	1 (rarely more)	1
	(2) Todea	usually 4	—	1
Marattiaceae	(1) Marattia	apparently 4	4 (or more)	1 (or more)
	(2) Angiopteris	4	4 (or more)	3 (or more)

From this it will be gathered that in the series of plants named,

[1] Angiospermen und Gymnospermen, p. 53, footnote 4.

the root is the first to depart from the simpler growth with a single initial, and even in *Todea* it appears to settle down into a definite type. The stem is the next to depart from the definite type of the simpler Ferns, while the apex of the leaf is most conservative in its characters, and even in *Marattia*, which shows greater complexity of apical construction both in root and stem, the leaf still shows, at least while young, a fairly regular segmentation from a single initial. This is, however, finally lost in *Angiopteris*. Thus there is not a strict parallelism of progression from the simpler to the more complex type of construction of the meristems, of a single species or individual, even within the series of plants specially examined.

Turning to other members of the Vascular Cryptogams, further exceptions are to be found, such as the Ophioglossaceae[1]: these being members of the Filicineous series, are for us at present the most important exceptions, and may be considered first. Here the apex both of root and stem appears to have a single initial; it is to be noted, however, that both these members are buried deeply underground in the living plant, and are so protected by their habit; but the leaf bearing the sporangia is aerial and exposed, and it is to be noted that its structure is comparatively bulky, and that in its early stages no single initial is found, while the sporangium is typically eusporangiate. Accordingly, it would appear that here there is a correlation even in the parts of an individual plant between exposure to dry air and a greater complexity of meristems on the one hand, and on the other between protection from evaporation and simplicity of structure of the meristems. But while recognising these facts, care must be taken that they be not overestimated. A comparison of the table above given will show that the case of the Ophioglossaceae is the exact converse of that for the Osmundaceae and Marattiaceae: in these the leaf which is aerial and exposed is the most conservative of the structure typical of

[1] See Holle, Bot. Zeit. 1875; as far as my own observations go, they bear out those of Holle.

the simpler forms, while in the Ophioglossaceae it is rather the root and stem which retain the simpler construction. This would therefore warn us of the danger of applying too closely in detail the correlation of exposed habit with increased meristematic complexity.

Again, in *Equisetum*, which is eusporangiate, the roots and stems have a single initial, with diagrammatically regular segmentation: it is to be noted that in these plants underground rhizomes are the rule, and it is only in their later stages of growth that the stems arise above ground. In many species of *Selaginella*, on the other hand, a single initial cell is formed in the sub-aerial stem; in other species there is a more complex structure of the meristem, while in *Lycopodium* three initials have been observed, though the general habit is similar to that of the allied Selaginellas. These notes will suffice to show that speaking of the Vascular Cryptogams as a whole, we are not in a position to state that there is any strict, invariable, and definite correlation of structure of meristems with exposed habit, or that there is any exact parallelism of progression in complexity in all the members of a given individual, species, or family. Still, I do not think that such exceptions as those above quoted invalidate my general conclusion that in the Filicineous series, taken as a whole, the progression of complexity of meristematic structure is to be taken as one index among others of the rise of the series from a semi-aquatic to a more distinctively sub-aerial habit, a conclusion which is borne out by comparison of the texture of the mature parts, and of the oophytes and sexual organs.

The texture of the leaves of the Ferns above studied, and their wings, present characters which deserve further remark, and especially we may draw a comparison between the 'filmy' Ferns, and their more robust neighbours. It has been repeatedly pointed out that the characters of submerged leaves of the higher plants, as distinct from subaerial leaves, are that they are thin, being composed of only few layers of cells; that stomata are absent; that there is no distinction of palisade and spongy parenchyma; and that the chlorophyll is

specially located in the superficial tissues, and much less plentiful within[1]. The chief differences of external condition between submerged and subaerial plants are, that transpiration is in the former impossible, and that they are less exposed to direct sunlight. Now these are also the conditions of plants which grow in shade, where the air is constantly near to the point of saturation with water; in them transpiration is at a minimum, while they receive only diffused sunlight. Accordingly a similarity of construction to that of water-plants may be expected, and it is clear that the leaves of the Hymenophyllaceae show more or less distinctly all the characters above noted, some of them even in a more marked degree than those of submerged Phanerogams. Further, while intercellular spaces are often large in submerged Phanerogams, they are entirely absent from the wings even of those filmy Ferns which are several layers in thickness. The 'filmy' texture is then to be regarded as an adaptive character, suited to life in a moist and shaded habitat.

But it is not found exclusively in the Hymenophyllaceae; *Asplenium resectum* and the *Leptopteris* section of the genus *Todea* show a similar texture of the frond, with absence of stomata and intercellular spaces, and with special location of the chlorophyll near the surface. I have shown that in the development of these filmy wings the segmentation of *Asplenium resectum* is that of the Polypodiaceae; also that that of the 'filmy' *Todeas* (which in every other respect correspond to other Osmundaceae) is at first like the latter, and that it is only in the later stages that a mode of segmentation is assumed which corresponds, and even then imperfectly, to that characteristic of the Hymenophyllaceae. Taking all the facts together, the general conclusion may be drawn that the 'filmy' texture is an adaptive character assumed by plants which live in shady and damp situations, and that it is not a safe indication of affinity; that while its most characteristic representatives are found among the Hymenophyllaceae, it has probably originated independently in at least three dis-

[1] Schenk, Vergl. Anat. d. subm. Gewächse, p. 3, and various other writers.

tinct divisions of the Ferns; viz. in the Hymenophyllaceae in which it is probably the typical structure; in species of *Asplenium* and of *Todea,* in which it is rather to be regarded as the result of a retrogressive adaptation.

An attempt has also been made in the above pages to make a comparative study of those wings which are so commonly found on the leaves of Ferns. It has generally been assumed that because those wing-structures which are continued, or decurrent from the leaf to the stem, are of irregular occurrence, therefore wings, whether on stem or on leaf, are of little morphological moment. This is an entirely fallacious conclusion. It is a matter of common observation that such wings are very constant in appearance and position on leaves of large classes of plants, more especially of the Ferns and Dicotyledons. Now one of the most important factors in stamping the morphological importance of any part is its constancy of occurrence and character in considerable series of organisms, and on this ground the wings deserve special attention. It may be objected, however, that wings are merely a natural consequence of the flattened development of leaves, and that an elongated and flattened structure must have two marginal lines of greatest curvature. This is true, but it does not diminish the interest of tracing those margins, comparing them in different plants, and noting their various modes of development in the different parts of the same leaf.

I have repeatedly dwelt upon the fact that though the leaves of the Filicineae may develop occasionally in a cylindrical form (*Pilularia*), or as spathulate structures without a midrib (*Drymoglossum*), those of the vast majority of them have a robust midrib, which is traversed longitudinally by two more or less developed lateral flanges or wings. These originate in the lowest Ferns from definite parts of the segments cut off from the apical cell, while in the higher, though their position is the same, the segmentation is less definite. In the mature state they usually show more robust and massive characters in the lower part of the leaf. This has been recognised both in external form, and in the internal struc-

ture in *Trichomanes reniforme*, in *Scolopendrium vulgare*, *Aspidium Filix mas*, *Asplenium nidus*, *Pteris aquilina*, and may be verified in most Ferns: more especially however is it to be noted in the higher Ferns of the series; and I have elsewhere pointed out[1] that the bulky developments which are found at the base of the leaf of *Osmunda* and *Todea*, and even the 'stipular' growths of the Marattiaceae are to be regarded as the result of metamorphosis, or special conformation of these wings, or of the extension of the growth across the face of the phyllopodium, so as to form the well-known commissure. There is thus a certain relation between the greater bulk of the base of the leaf, and that of the wings which it bears; but the wings of the lower part, though of bulky development, are but little expanded in area. In that part of the phyllopodium which is usually distinguished as the petiole, the wings are of a reduced type, and are seen merely as pale streaks, often discontinuous, which run down the sides of the petiole, and, though they may not project at all, these streaks show where the morphological margin of the leaf lies; sometimes, however, the wings project even here as distinct flanges (many Hymenophyllaceae). It is, however, in the upper part of the leaf that the wings attain their typical development, and there they constitute the large proportion of the expanded surface, whether of the simple or the branched leaf. Thus the wings are subject to great differences of development in different parts of the leaf, and indeed the general conformation of the different parts of the leaf depends more closely upon this than upon differences of development of the thickened midrib. It is also a matter of common experience that from them arise the branchings of the leaf.

It will be recognised that this mode of viewing the leaf throughout its length as a whole, and avoiding at the outset those horizontal distinctions into 'foliar base' and 'upper leaf,' which are habitual with other writers, naturally leads to a more coherent view of the real nature of the leaf. It is typically a flattened structure, of which the longitudinal lines

[1] Phil. Trans. 1884, Part II, pp. 578, etc.

of greatest curvature, or margins, are subject to various development in different parts, and are the seat of the branchings of a higher order.

The meristems of the various parts having been investigated in a series of plants which bridges over the transition from growth with a single initial to growth with several, it is to be expected that some light may have been thrown upon the problem of the real nature of the apical cell, and of the causes which bring about so remarkable a construction as that where there is a regular segmentation from an initial of definite form. Though the solution of the problem is not yet to hand, certain interesting conclusions may be drawn from a comparison of the plants studied [1].

The comparison of Figs. 3 and 4 of roots, and of Figs. 39 and 43 of leaves, shows, in place of a single three-sided initial, three initials so arranged, together with their segments, as to correspond to what is seen in transverse section through segments immediately below a typical three-sided apical cell. Thus both in certain roots and in certain leaves there may be seen a construction which is the equivalent of the continuation of the typical system of construction upwards into that space (the apical cell), which is usually unsegmented. This I take to be evidence supporting the view of Sachs that the apical cell is but a gap in the system of construction: though in other cases (Figs. 12, 25, 27, 28) the arrangement of the walls is not according to the exact type, still I think the conclusion is justified that the difference between growth with one initial and with several initials is due to the greater completeness in the latter case of the system of walls.

It is obvious that not only the apex of the average root, but also those of stem and leaf are more bulky in the higher terms of our series than in the more slender, lower terms:

[1] Sachs, in his well-known paper 'Ueber Zellanordnung und Wachsthum' (Arbeiten, Vol. II, p. 200), writes in connection with the partitioning off of the interior of plants by cell-divisions and its relation to growth as follows:—'The acquisition of a cellular character of the interior is accordingly an independent phenomenon, the cause of which we are as little aware of as that of growth itself: but from what has been said, it must necessarily be subordinated to growth.'

and the suggestion appears ready to hand that the greater complexity of structure depends directly upon, or is at least closely connected with, the greater bulk. This point I have already discussed elsewhere as regards the root[1], and the conclusion there arrived at for the root is equally applicable to stems, leaves, and wings of the leaf of the Ferns examined. That conclusion is this: — That greater size of a member does not entail greater complexity of meristem in members of the same individual plant, or of plants of the same species; for instance, roots, etc. of smaller size may have a more complex meristem than larger roots (*Osmunda*): but such a correlation may be traced to some degree in different species of the same genus (stems of *Selaginella*), and it is plainly to be seen on comparison of the corresponding parts of plants less closely related. In comparing corresponding parts of plants not in the same genus or division of Ferns, a certain relation between bulk and complexity of meristematic structure is obviously seen, and this has been referred to so constantly throughout this paper that it need not be farther dwelt upon here. On the other hand, the comparison of the mode of development of the wings plainly shows that actual size does not directly dominate the mode of segmentation within narrow limits of affinity: the bulky leaf of *Trichomanes reniforme* (Fig. 51), notwithstanding its thickness, retains the simple mode of segmentation of its genus: the thin filmy leaf of *Asplenium resectum* (Fig. 58), notwithstanding that it is actually much less bulky than the above, retains the more complicated segmentation of the Polypodiaceae. Both of these show, independently of actual size, a conservatism of their family type of segmentation, and though I would not be prepared, on the narrow ground of observation as yet before us, to state as a general principle that such conservatism or hereditary character is of common occurrence, such examples as these are sufficient to show that those who state that the arrangement of cell-walls has

[1] Quart. Journ. Micr. Sci. 1885, pp. 88, 98–99.

actually no systematic importance have gone too far[1]. The whole argument of this paper is based on comparison of meristems: it has been shown that the progressive characters of the meristems run parallel with other systematic characters of the Filicineous series, and accordingly they must themselves be recognised as having a systematic value. The fault in dealing with meristems as systematic evidence has been the abuse of them: that is, however, no sufficient reason for ignoring entirely their systematic value.

Not only are the meristems of the higher members of this series more bulky, and the external surface less strongly curved, but they are also notable for their extremely watery character, their very thin cell-walls, and the relatively large size of the individual cells. These characters mark the meristems out as badly nourished, and they present a most striking contrast to the small-celled, densely-protoplasmic and largely-nucleated meristems of the Phanerogams, notwithstanding that in respect of their segmentation they approach them. It may even be suggested that the poverty of the tissue and the size of the cells composing it may have a connection as cause and effect, the substance necessary for the formation of more numerous walls and nuclei not being at hand: and reflections such as these would lead us on to consider whether the presence of an apical cell with a regular segmentation may not have its origin in some phenomena of nutrition not yet clearly recognised. We might with some show of probability assume that the regularity of segmentation depended upon the regularity of supply of wall-forming substance from the several sides of the meristems. Such regularity of supply would be most easily maintained where the whole apex is of small size, while in the larger apices the stream of nourishment would be less likely to converge equally from all sides upon the central point, and irregularity of construction would be the result: this is in accordance with experience, for, speaking generally, the smaller apices of the Filicineous series have as a rule a single initial, while the

[1] Compare Goebel. Sachs' Arbeiten II., p. 451.

larger are less regular in their segmentation. I do not consider that this suggestion is by any means established by my observations on the Ferns, but the result of the examination of a very considerable number of meristems makes me think that some such connection between nutrition and meristematic construction is not improbable.

In this connection two other points deserve notice: the first is, that where a single initial is found in the relatively bulky meristems of the plants higher in the series, the segments cut off from it increase more rapidly in size as compared with the apical cell itself than in the lower terms of the series. (Compare Figs 22, 23, 24, of stems, and Figs. 35, 36, 37, 38, of leaves). The second is, that in the course of this growth, the subdivisions of the segments are far from being regular: often cells which I have styled 'secondary initials' make their appearance in the segments, and appear to undergo subdivisions which show some similarity to those of the apical cell itself (compare Figs. 34, 36, 38, 41, the cells marked *o*; also Fig. 7). If, as above suggested, the regularity of segmentation depend upon the regularity of the nutritive supply, these irregularities of subdivision of the segments and the appearance of the 'secondary initials' point to such want of uniformity of supply as may be expected to have its effect also upon the initial cell itself. With regard to these 'secondary initials' a comparison may be drawn to the meristematic arrangements of *Psilotum* as represented by Graf. Solms[1]; his account of the appearance, disappearance, and renewal of initial cells goes far to break down too formal ideas as to the importance and supremacy of the apical cell itself.

The general results of these investigations as regards phylogeny are to demonstrate, more clearly than before, that the Filicineae constitute a natural series, illustrating an adaptive sequence from plants of semi-aquatic to those of a more dry habit; to show that additional evidence only tends to fix the Osmundaceae still more firmly than before in the position of a link bridging over the gap between the leptosporangiate and

[1] Ann. d. Jard. Bot. d. Buitenzorg, Vol. IV, 1884, Plate XXI, Figs. 1, etc.

eusporangiate Ferns; and to strengthen the bond between them and the Marattiaceae. A reference to the table of meristems given above (p. 376) shows further that in these characters *Todea* stands nearer to the latter than *Osmunda*, and this conclusion is further borne out by the presence of the commissure at the base of the leaf. On the other hand, as regards the meristems, *Marattia* appears to be nearer to the Osmundaceae than is *Angiopteris*; thus on the basis of the meristems the series of genera would be *Osmunda*, *Todea*, *Marattia*, *Angiopteris*. It is, however, to be noted that the coalescence of the sporangia is less complete in *Angiopteris* than in *Marattia*.

It remains to remark on the probable relation of this Filicineous series to other forms. There is, I think, every reason to believe that the Hymenophyllaceae are of Algal-Bryophytic origin, and they probably arose from some forms intermediate between our present green Algae and the Bryophyta, but not directly from either as we now see them; the position of the Hydropterideae (the only heterosporous Ferns) is probably in relation rather to the lower terms of the homosporous series than to the higher ones. Then, as regards the vegetative organs of the sporophyte, whether we take external form, internal structure, or development into account, the relation of the highest Pteridophyta (Marattiaceae and Ophioglossaceae) to the Cycadaceae is undeniable; but between these, as regards reproduction, there is the vital difference between the homosporous zooidogam and the heterosporous siphonogam. Though there is no reason to assume that progress in vegetative structure and in sexual differentiation has necessarily taken place simultaneously, still, this is a very serious gap, and from the point of view of phylogeny it is very desirable to find some heterosporous form allied to the Marattiaceae, which should serve as a connecting link. Approaching the matter from the point of view of the characters of the leaf, I appended the following note to a paper written in 1884[1]:—'The leaf of *Isoetes* shows intermediate characters between those of *Angiopteris*

[1] Phil. Tran. 1884, Part II, p. 610.

and of the Cycadaceae. There is no apical cell, and apical growth is not strongly defined; periclinal divisions of the superficial cells are frequent throughout the leaf, from apex to base, but especially on the ventral side; intercalary growth is strongest at first below the ligule, and then diminishes in that part and extends to the upper part of the leaf. These characters, as well as others, suggest that *Isoetes* may be a form intermediate between Marattiaceae and Cycadaceae, in which the vegetative organs have been reduced in structure and external form in accordance with aqueous habit.' Since then, Vines[1] has on various grounds arrived at the conclusion that the true relation of *Isoetes* is rather to the Filicineae than to the Lycopodineae. Without at present entering upon the discussion of this matter at large, it will be well to point out the bearing of the observations contained in this paper upon this debateable question. So far as they affect the point, they strengthen rather than invalidate the suggested grounds of affinity of *Isoetes* to the Marattiaceae. It has been shown by Bruchmann that the apices of the roots of *Isoetes* have a stratified structure, similar to that which is seen in certain Angiosperms, there being present no clearly defined initial cells. The same writer, and also Hegelmaier[2], point out that the apex of the stem is occupied by a small number of initial cells, which appear to correspond to the structure found in the Marattiaceae. I have also indicated that the characters of the leaf are not inconsistent with the suggested position, and Hegelmaier[3] also points out that there is no apical cell. As regards the form of the leaf, when it is remembered that the leaves of the *Danaeas* are relatively simple in conformation, while in *D. simplicifolia*, Rudge, the leaf is actually unbranched[4], it will be seen that comparatively slight simplification of the type of leaf would result in such a one as that of *Isoetes*. Taking all the meristematic characters together (and it is with them that we are now more especially concerned), the evidence offers no serious barrier to assigning to *Isoetes* the position

[1] Annals of Botany, II, pp. 117, 223. [2] Bot. Zeit. 1875, pp. 485–6.
[3] l. c. p. 499. [4] Kunze, Die Farrnkräuter, Plate 50.

suggested by Vines. But, on the other hand, it may be argued that such evidence would be equally strongly in favour of a Lycopodinous affinity; and I anticipate that a knowledge even of minutest details of the meristems will not suffice to decide this interesting question. A final conclusion will have to be based on the broadest possible comparative grounds.

POSTSCRIPT.

Since the above was in type, the comprehensive work by MM. Van Tieghem and Doulist has come to my hands, in which the authors state (footnote, page 379) that there is only one initial cell at the apex of the root in *Todea* 'as in other ferns.' It will be no surprise to me to find that in certain cases *Todea barbare* has a structure at the apex of the root more closely resembling that of the typical ferns than that which I have described. It will be noticed that I lay down no type of structure in *Todea* and *Osmunda*, but point out rather that 'there is no such strict uniformity in these plants as is found in the roots of typically leptosporangiate ferns (above, p. 284); thus the reference of the whole meristem of *Todea* in certain cases to a single initial cell does not affect the general argument, so long as it is recognised that a system of construction occurs not infrequently in these plants, such as I have described and figured, which is more complex than that which is so regular and prevalent in the Leptosporangiate Ferns.

DESCRIPTION OF FIGURES IN PLATES XX, XXI, XXII, XXIII, & XXIV.

Illustrating Professor F. O. Bower's paper on the Comparative Examination of the Meristems of Ferns as a Phylogenetic Study.

ROOTS.

Fig. 1. Scheme of construction of the apex of the root with a three-sided pyramidal apical cell, quoted from Sachs's Arbeiten, Bd. II, Taf. III, Fig. 12.

Roots of *Osmunda regalis*, Figs. 2–4, and 6–11 (×216).

Fig. 2. Transverse section of apex of root with a three-sided initial, but the segments not regular.

Fig. 3. Ditto. Three initial cells (*x*) separated by principal walls *p*, *p*. The sextant walls are marked *s*, *s*.

Fig. 4. Transverse section immediately below the root-cap, showing three initials (*x*): the dotted line is a cell-division in the root-cap, seen on focussing deeply, and this shows that the section has passed through the initials, and is not below them.

Fig. 5. Quoted from Naegeli and Leitgeb, Taf. XIV, Fig. 5, a transverse section of the apex of the root of *Pteris hastata*, as seen by focussing below the apical cell. *p*, *p*, the principal walls. *s*, *s*, the sextant walls. Compare this, which is an optical section through the segments below the initial, with Figs. 3, 4, which are sections through the initials of *Osmunda*.

Fig. 6. Median longitudinal section, with pyramidal apical cell. *tr*, cells developing as tracheides.

Fig. 7. A very irregular meristem, with a pyramidal apical cell (*x*). Segments undergoing repeated periclinal division.

Fig. 8. Two oblong initial cells (*x*, *x*): segments are cut off by periclinal walls from both ends of them, and by anticlinals from their sides.

Fig. 9. Two similar initials with their segments.

Fig. 10. Young lateral root with two oblong initials. *xy*, the xylem of the main root. *p*, the pericambium.

Fig. 11. Apex of a young lateral root in longitudinal section.

Roots of *Todea barbara*, Figs. 12–16 (×216).

Fig. 12. A very regular meristem in transverse section, showing four initials (*x*, *x*).

Fig. 13. Apex of root in longitudinal section, showing two pyramidal initials.

Fig. 14. Ditto, with two oblong initials.

Fig. 15. Group of cells derived from one rhizogenic cell of the endodermis showing two oblong initials (*x*, *x*).

Fig. 16. Apex of a rather older lateral root with two pyramidal initials (*x*, *x*).

Fig. 17. Scheme of construction of a root of the Marattiaceous or coaxial type. *AA*, axis; *aa*, anticlinals; *pp*, periclinals; *xx*, initial cells.

STEMS.

Trichomanes radicans, Figs. 18–21.

Fig. 18. Longitudinal section through the apex (×35): *ap*, the apex. *ax*, the axillary bud. *l*, the leaf.

Fig. 19. Transverse section showing apical meristem in plan: *l*, young leaf. The arrows indicate the vertical direction as the plant grew (×130).

Fig. 20. Longitudinal section of the apex of the stem (×130).

Fig. 21. A very young axillary bud in longitudinal section: the arrow indicates the direction of the apex of the main axis (×130).

Amphicosmia Walkerae.

Fig. 22. Apical meristem of stem seen in plan (×130).

Osmunda regalis, Figs. 23–26 (×130).

Fig. 23. Apex of stem seen in plan. *l*, young leaf. *l'*, *l'*, older leaves. Initial (*x*) of regular form, segmentation regular.

Fig. 24. Ditto, initial less regular in form, and segmentation less regular.

Fig. 25. Ditto, apparently no single initial.

Fig. 26. Apex in median longitudinal section: the succession of segments is not clearly to be seen.

Angiopteris evecta, Figs. 27–29 (×130).

Fig. 27. Apex of stem seen in plan (×130): apparently four initials (*x*, *x*).

Fig. 29. Apex of stem in median longitudinal section.

Marattia fraxinea.

Fig. 28. Apex of stem as seen in plan: the number of initials is uncertain (×130).

LEAVES.

Trichomanes radicans, Figs. 30–32.

Fig. 30. Young leaf as seen from above when projecting only slightly from the surface of the stem: the arrow points to the apex of the stem: *m*, *m* = marginal cells. (×163).

Fig. 31. Part of a tangential section of the stem, passing vertically through a young leaf, and showing its first segmentations (×130).

Fig. 32. Median longitudinal section of leaf: the arrow indicates the direction of the apex of the stem (×130).

Trichomanes reniforme.

Fig. 33. Apex of the leaf showing the T division of the initial cell, the identity of which is thus lost. (×130).

Osmunda regalis, Figs. 34–35.

Fig. 34. Apex of leaf seen in plan. *s*, sextant walls. *o*, partial initial. The arrow shows in this and subsequent figures the direction of the apex of the stem.

Fig. 35. Median longitudinal section of the apex of a leaf.

Marattia fraxinea, Figs. 36–41 (×130).

Fig. 36. Apex of leaf seen in plan : *o*, *o*, partial initials.
Fig. 37. Ditto, from a young leaf with no pinnae.
Fig. 38. Ditto, from a young leaf.
Fig. 39. Ditto, but no single initial cell is to be seen : from a leaf on which some pinnae were already formed.
Fig. 40. Apex of a young leaf in median longitudinal section. *o*, a partial initial.
Fig. 41. Ditto, the segmentation of the partial initial (*o*) has shown some regularity. *x*, is the apical cell.

Angiopteris evecta, Figs. 42–45 (×130).

Fig. 42. Apex of leaf seen in plan. *p*, principal wall.
Fig. 43. Ditto. *o*, partial initials. *p*, principal wall.
Fig. 44. Apex of leaf in median longitudinal section. *p*, principal wall.
Fig. 45. Ditto.

WINGS OF THE LEAF.

Trichomanes radicans, Figs. 46–49 (×325).

Fig. 46. Young wing as seen in a transverse section of the phyllopodium. *m*, the marginal cell.
Fig. 47. Ditto, rather older.
Fig. 48. Ditto, more advanced.
Fig. 49. Marginal series of cells (*m*, *m*) seen from without. *h*, *h*, hairs.

Trichomanes reniforme, Figs. 50–51 (×325).

Fig. 50. Wing as seen in a transverse section near to the base of the leaf: segmentation of the marginal cell (*m*) of the polypodiaceous type.
Fig. 51. Transverse section through the young lamina, showing the large marginal cell (*m*) with regular transverse segmentation (compare Figs. 46-48).

Hymenophyllum dilatatum, Figs. 52–54 (×325).

Fig. 52. Wing as seen in transverse section of the young petiole: compare Fig. 51.
Figs. 53–54. Irregular segmentations at the close of the functional activity of the marginal cells.

Pteris cretica.

Fig. 55. Wing as seen in a transverse section of a pinna. (×325.)

Scolopendrium vulgare.

Fig. 56. Wing as seen in a transverse section of the young leaf near its apex. *m*, marginal cell. (×325.)
Fig. 57. Ditto, more advanced. (×325.)

Asplenium resectum.

Fig. 58. Transverse section through a young pinna, showing, notwithstanding the filmy character of the frond, the same marginal segmentation as in *Pteris* and *Scolopendrium*. (×325.)

Todea barbara.

Fig. 59. Surface view of the margin of a pinnule: the arrow points to the apex of the pinnule. (×325.)

Fig. 60. Young wing as seen in transverse section (×325).

Todea superba, Figs. 61–67 (×325).

Figs. 61, 63, 65. Young wings as seen in the transverse sections of very young pinnules.

Figs. 62, 64, 66, 67. Wings as seen in transverse sections of pinnules, and showing the variability of segmentation.

Todea hymenophylloides, Figs. 68–69.

Figs. 68, 69. Young wings as seen in transverse sections of the pinnules (×325).

Angiopteris evecta, Figs. 70–73 (×325).

Fig. 70. Transverse section of a very young pinnule, showing the first origin of a wing at *.

Figs. 71, 72, 73. Older wings as seen in transverse section, and illustrating their mode of segmentation, and the absence of definite marginal cells.

SPORANGIA.

Osmunda regalis, Figs. 74–82.

Fig. 74. First origin of a sporangium as seen in a transverse section of a young pinnule (×550).

Fig. 75. Three sporangia rather more advanced (×325).

Figs. 76–82. A series of sporangia cut in longitudinal section, illustrating the development, and also those irregularities of segmentation, which are commonly found. The most frequent type is that shown in Fig. 77 (×325).

Todea barbara, Figs. 83–87.

Fig. 83. Early stages of development of two sporangia as seen in transverse section of a pinnule (×550).

Figs. 84, 85. Young sporangia as seen in surface view (×550).

Figs. 86, 87. Sporangia in longitudinal section, showing different modes of segmentation. Fig. 86 is the commoner type (×550).

Fig. 88, *a–g*. A series of diagrammatic figures, constructed from drawings of the sporangia of different members of the Filicineous series.

a. Sporangium of the *Polypodiaceae* (compare Reess, Pringsh. Jahrb. Tom. V, Taf. XXI, XXII).

b. Sporangium of the *Hymenophyllaceae* (compare Prantl, Hymenophyllaceae, Taf. VI, Figs. 100*c*, 104).

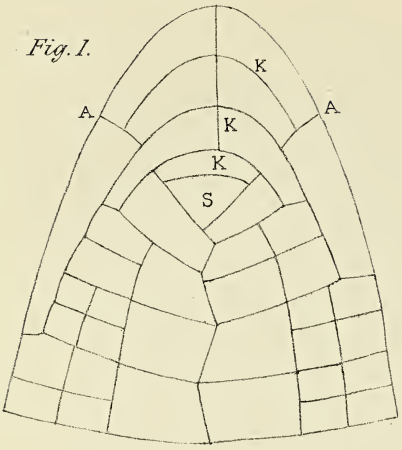
c. Sporangium of *Schizaeaceae* (compare Prantl, Schizaeaceae, Taf. VI, Fig. 91).

d. Sporangium of *Osmundaceae*: diagram constructed from comparison of a number of specimens (compare Fig. 87 of *Todea*, and Fig. 75 of *Osmunda*).

e. Sporangium of *Todea barbara*, in which the archesporium has a square base (compare Figs. 83, 86).

f and *g*. Sporangia of *Angiopteris* (compare Goebel, Bot. Zeit. 1877, Taf. VI, Figs. 3, 4).

Fig. 1.



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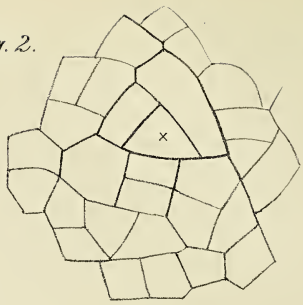

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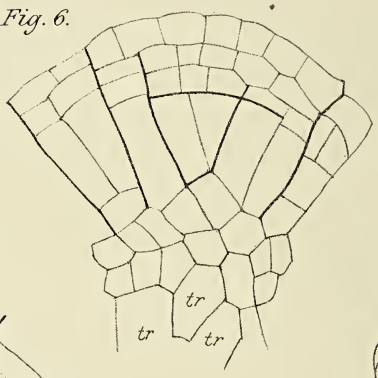

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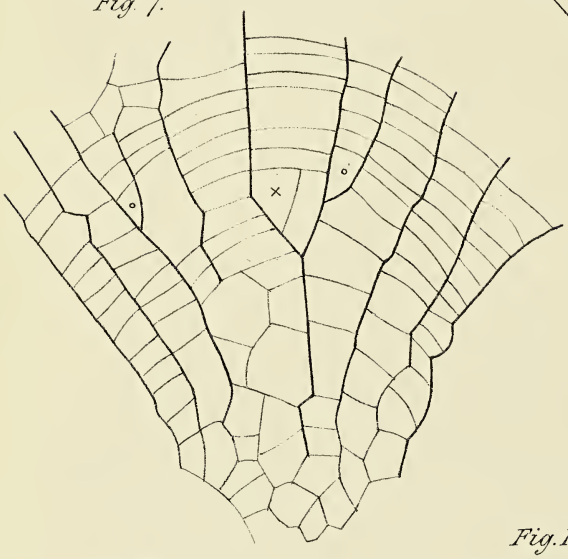

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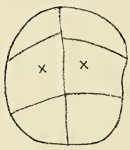

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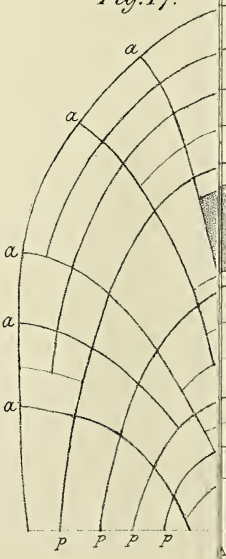

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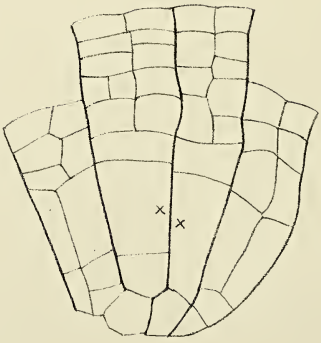

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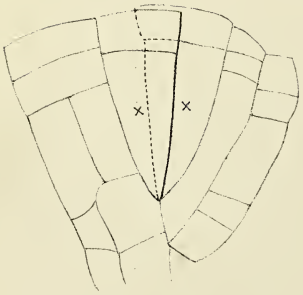

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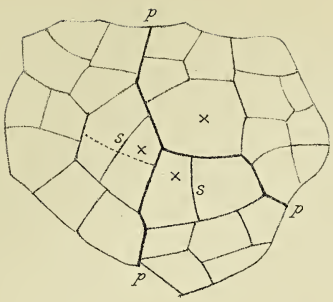

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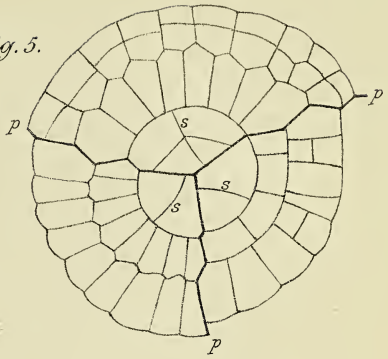

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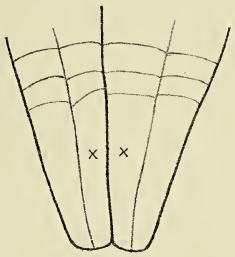

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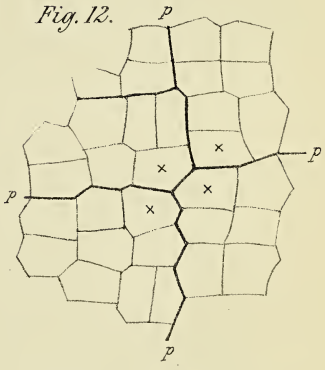

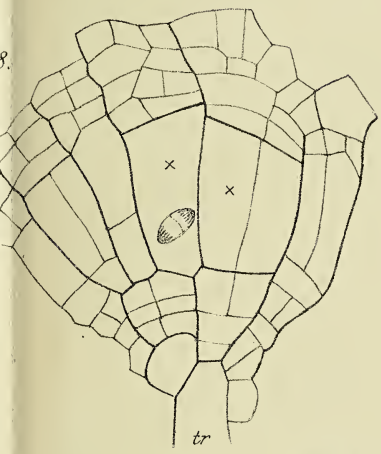

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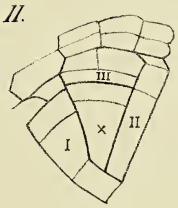

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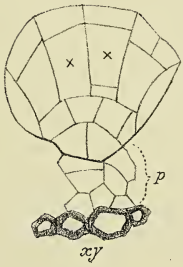

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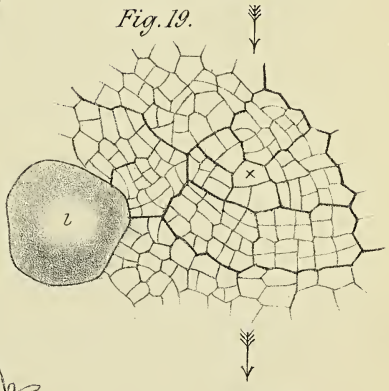

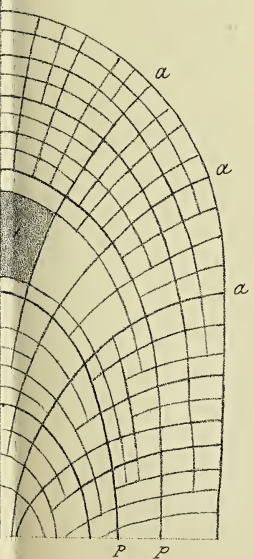

Fig. 18.

Fig. 21.

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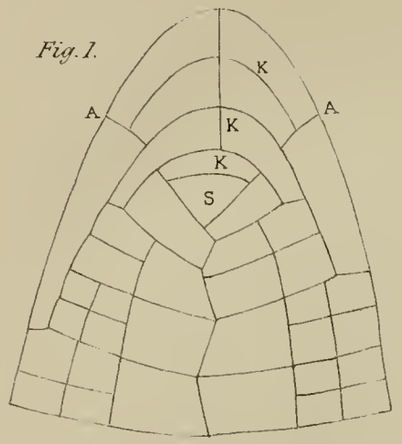
Fig. 1.



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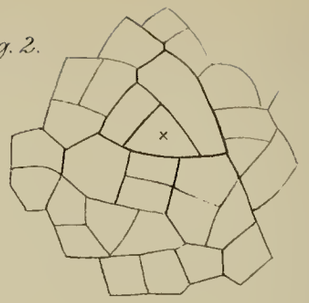

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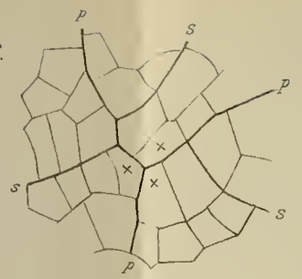

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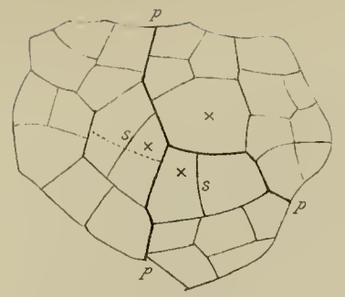

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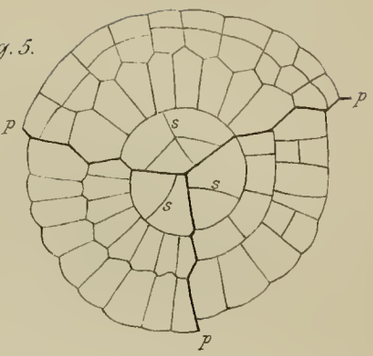

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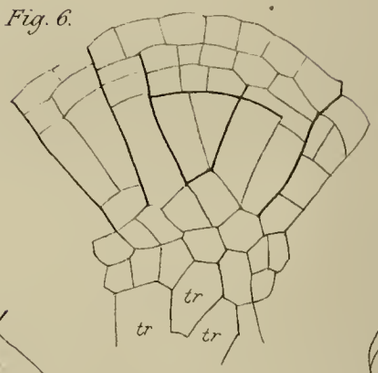

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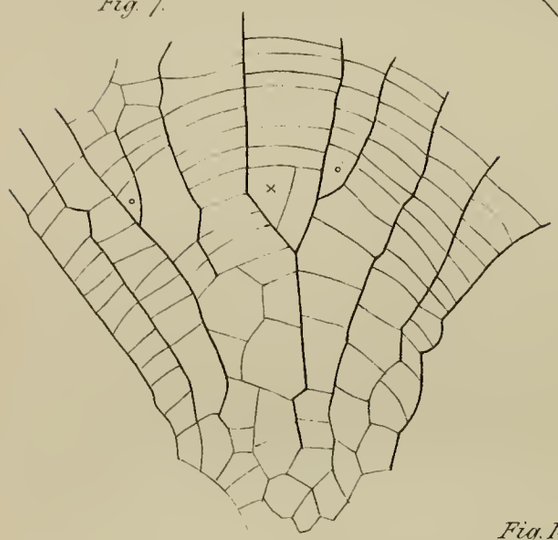

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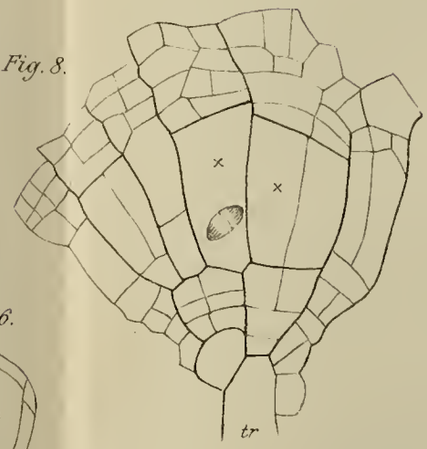

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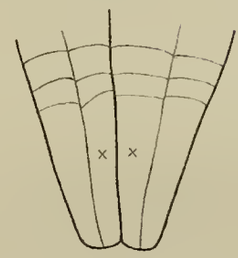

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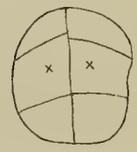

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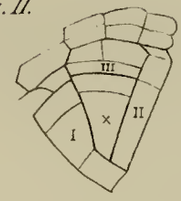

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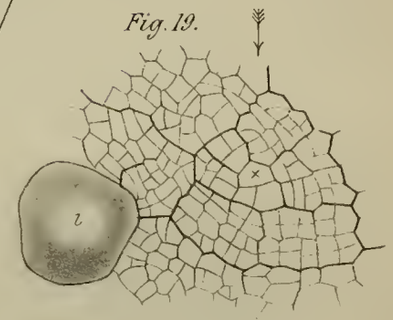
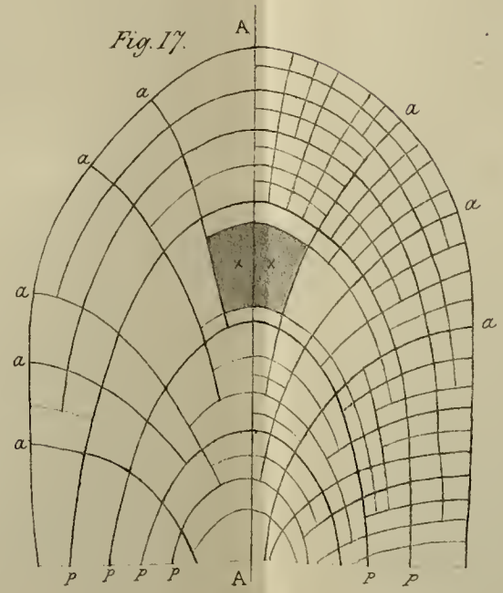


Fig. 17.



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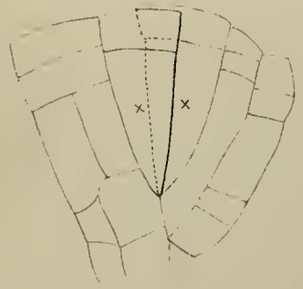

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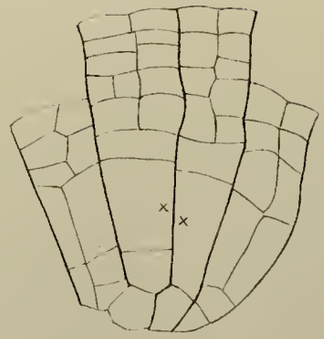

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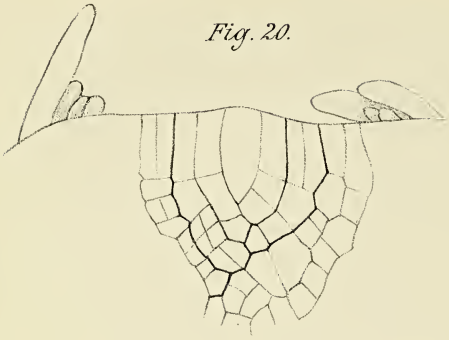
Fig. 20.



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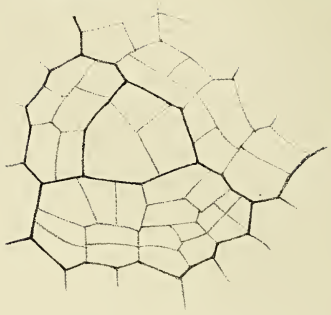

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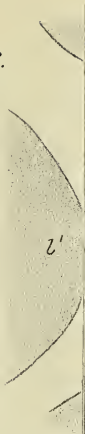

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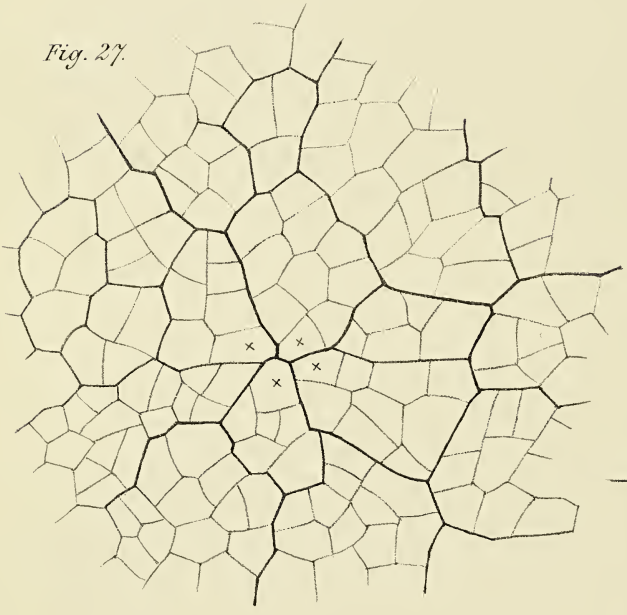

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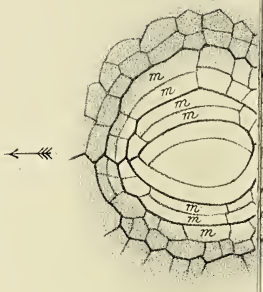

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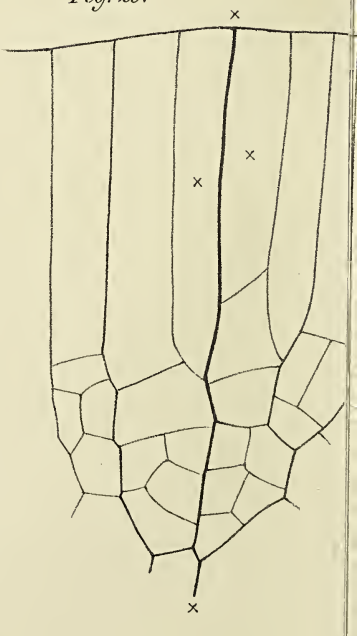

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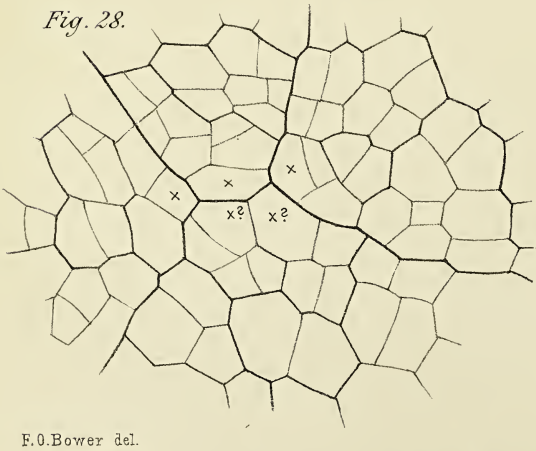

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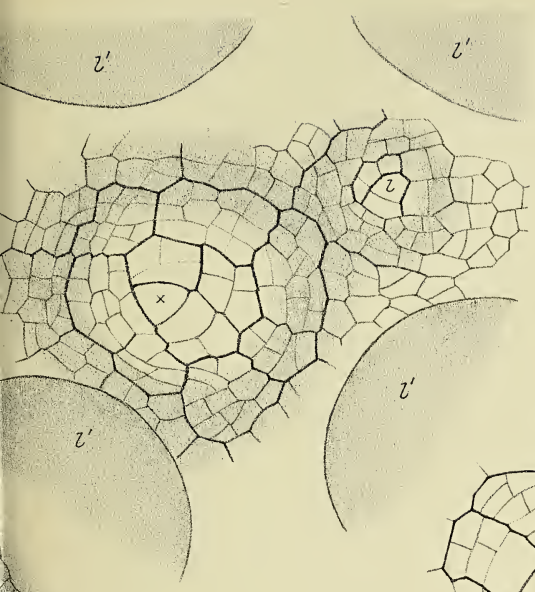

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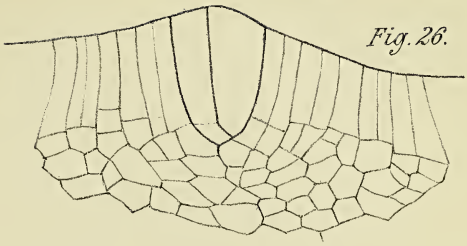

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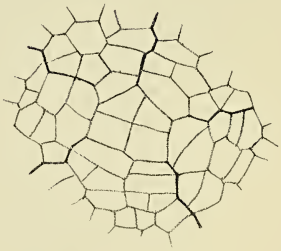

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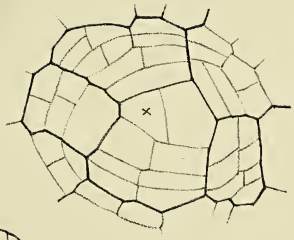

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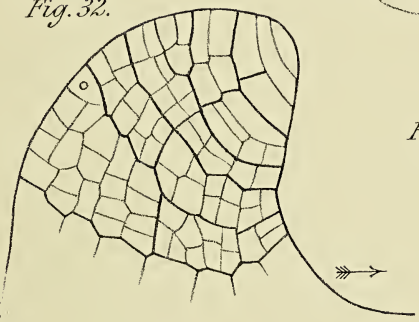

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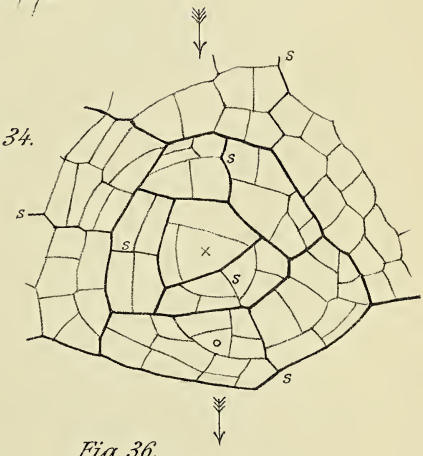

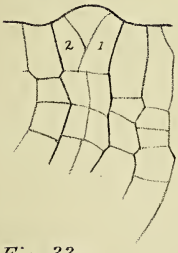

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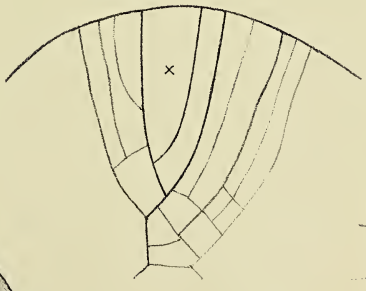

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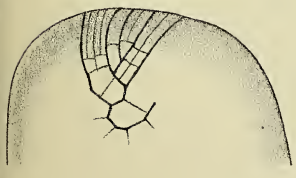

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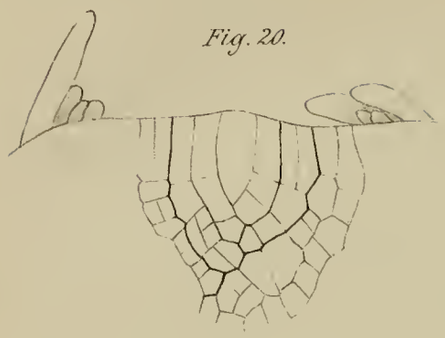

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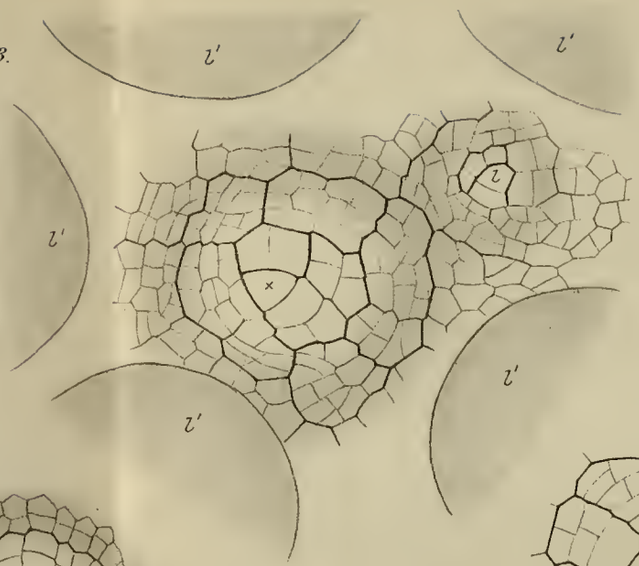

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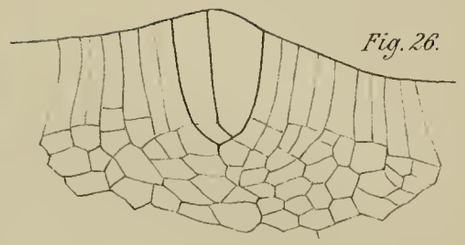

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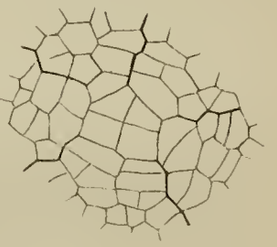

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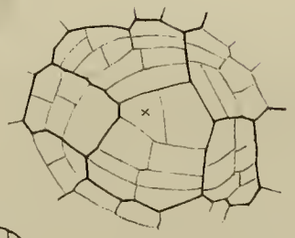

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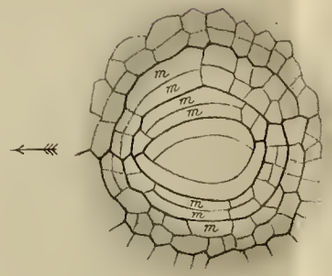

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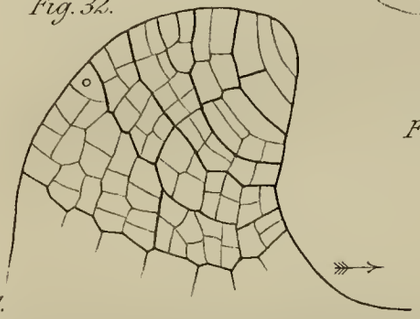

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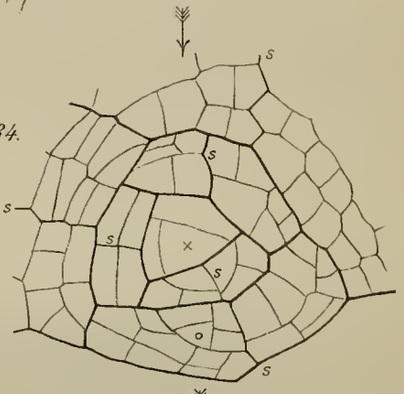

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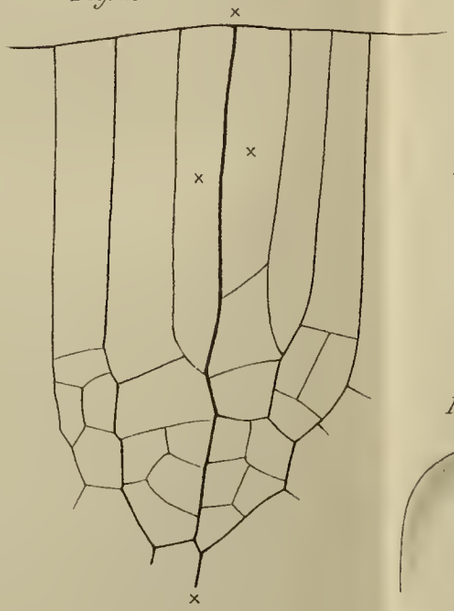

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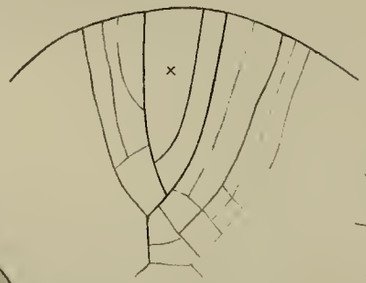

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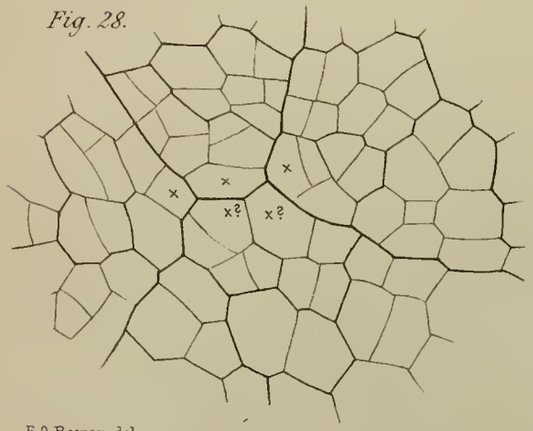

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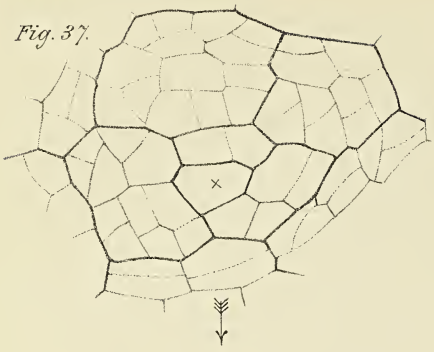

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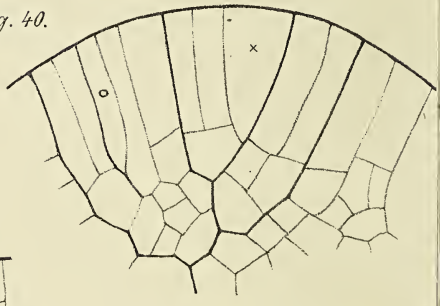

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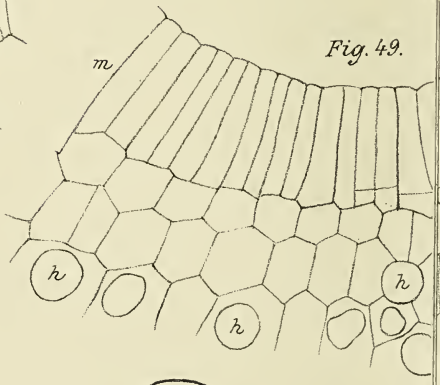

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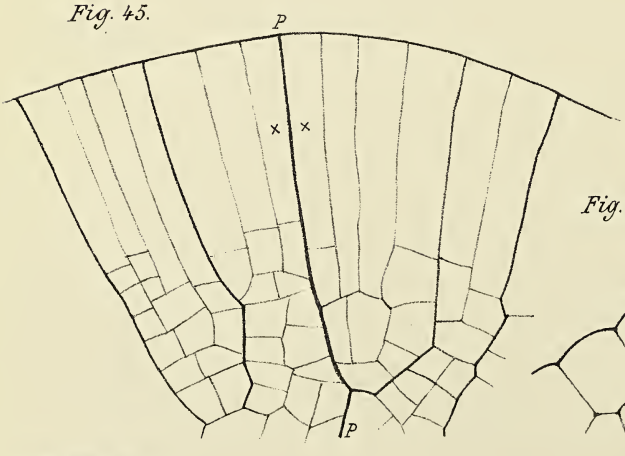

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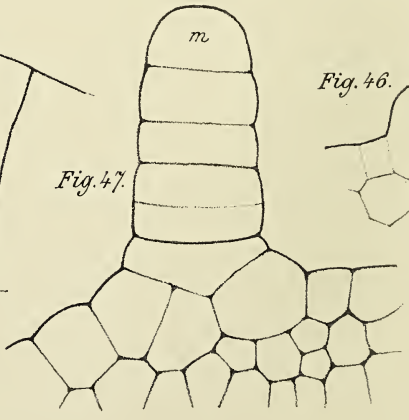

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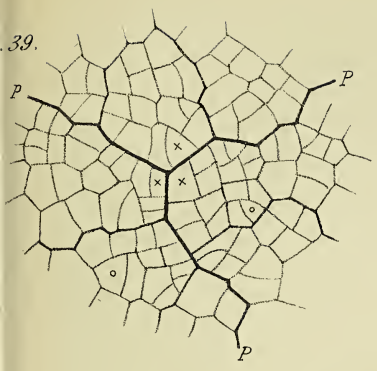

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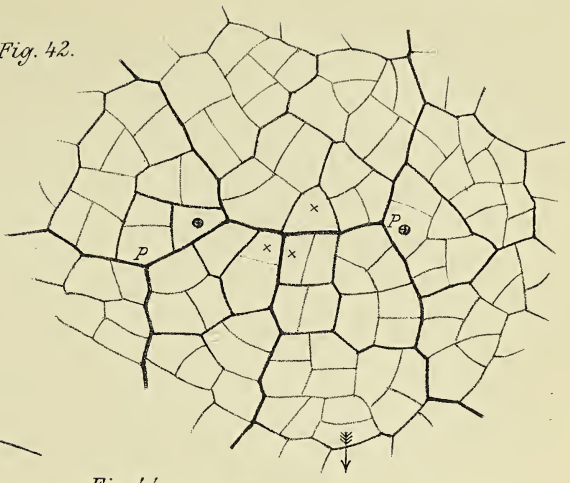

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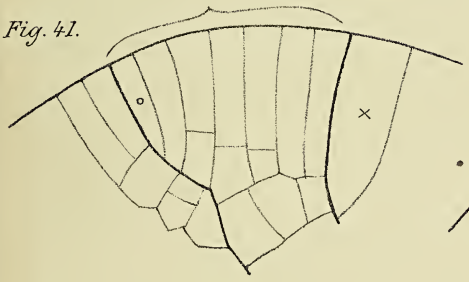

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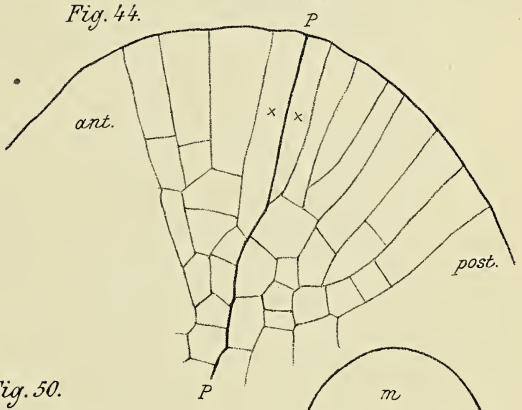

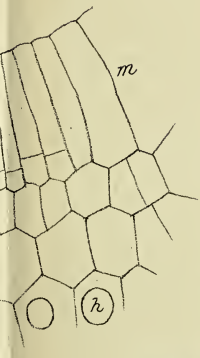

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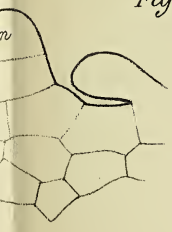

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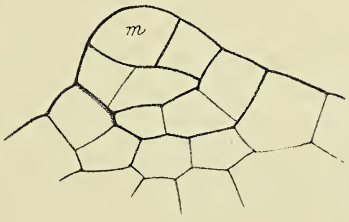

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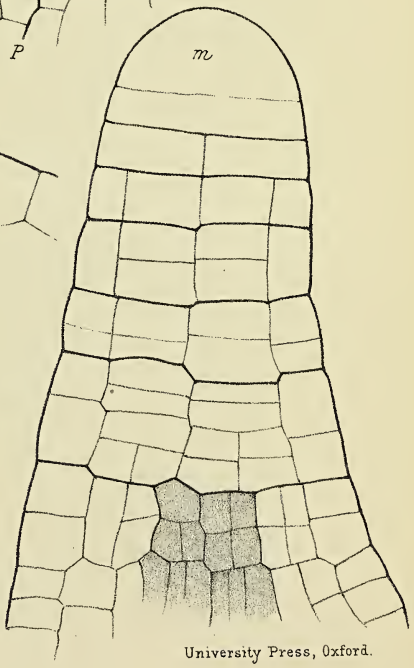

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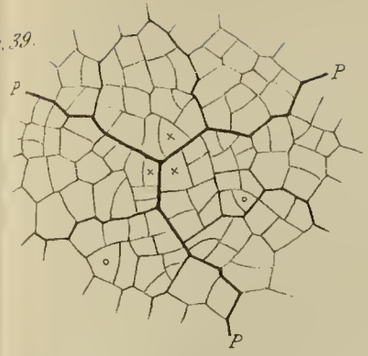

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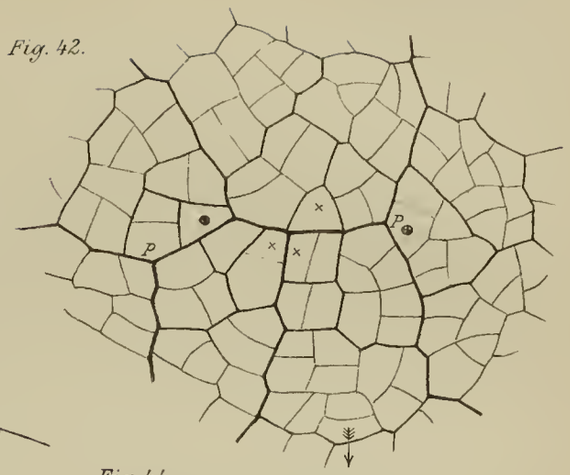

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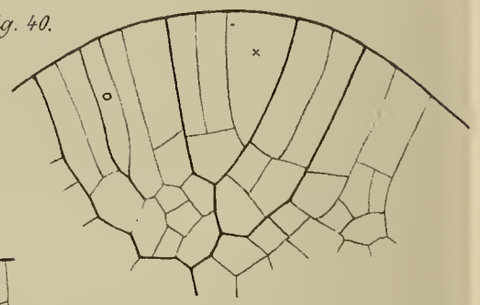

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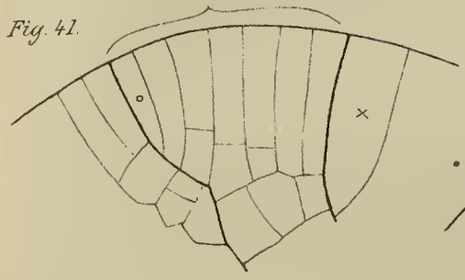

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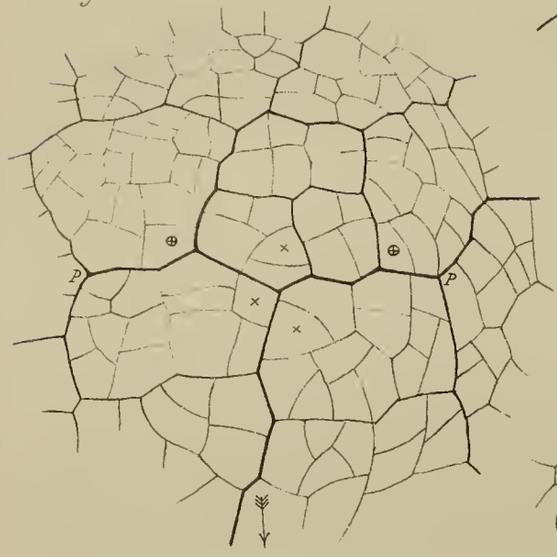

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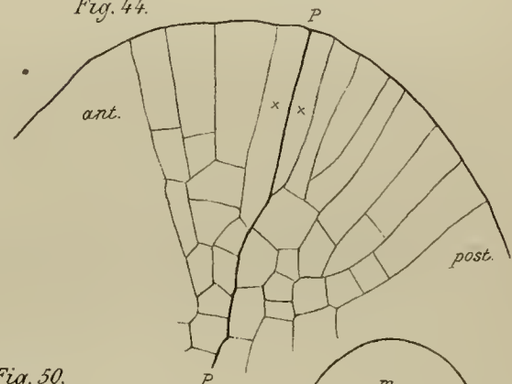

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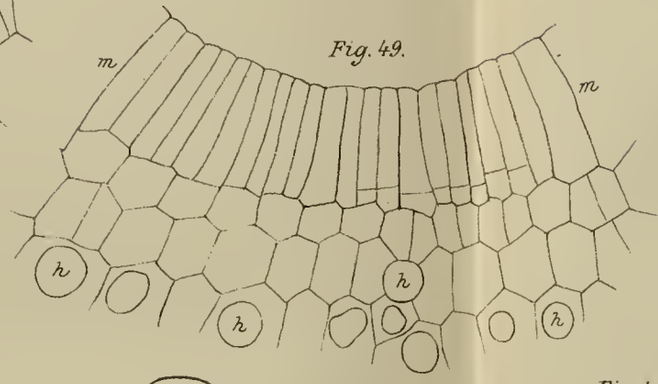

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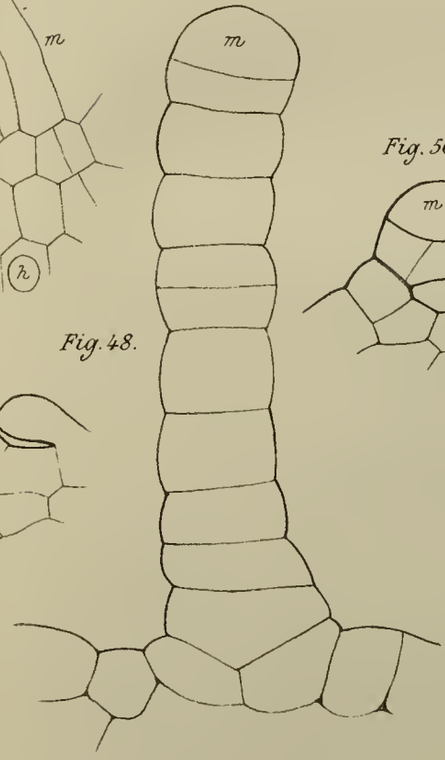

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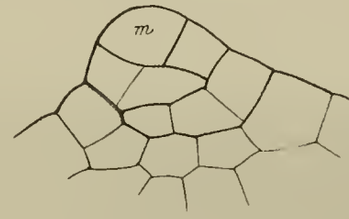

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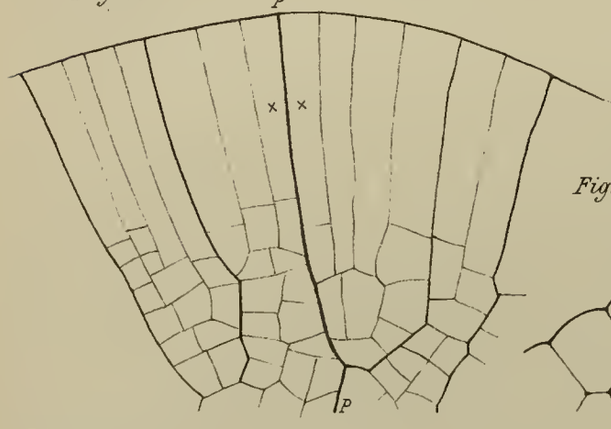

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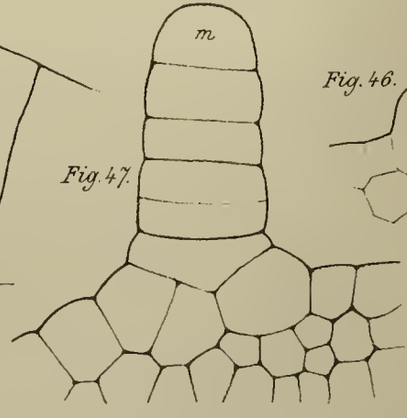

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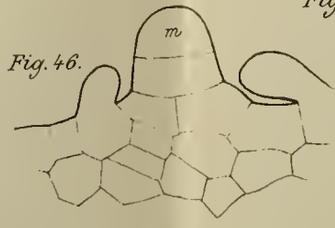

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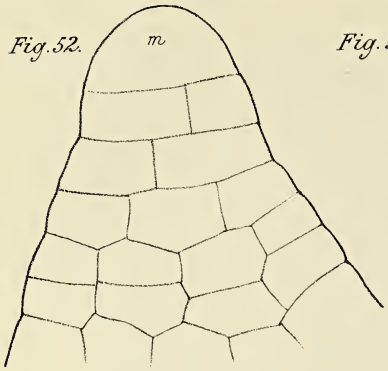

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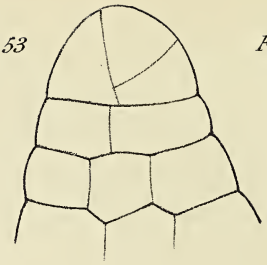

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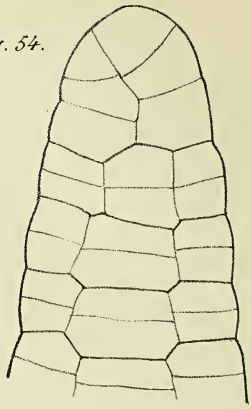

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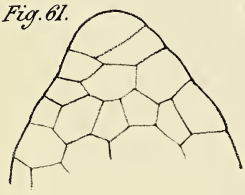

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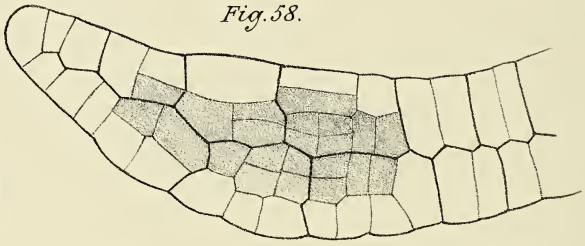

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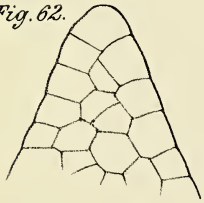

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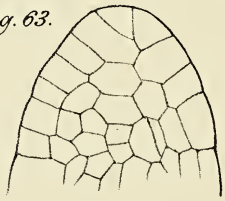

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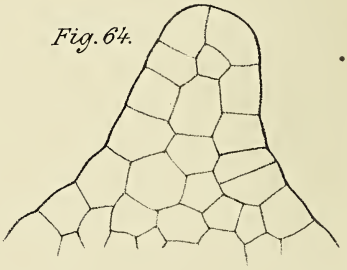

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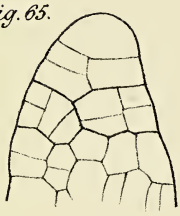

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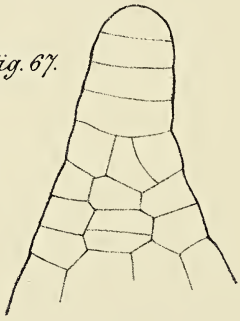

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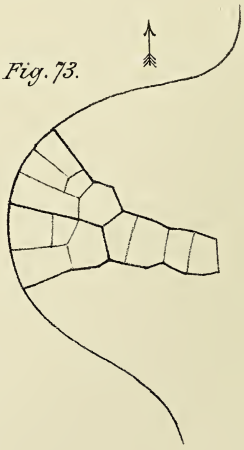

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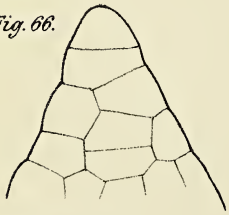

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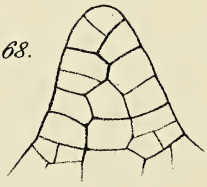

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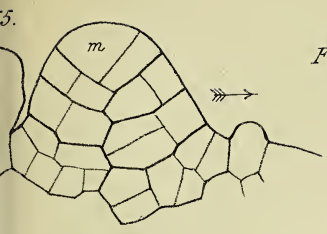

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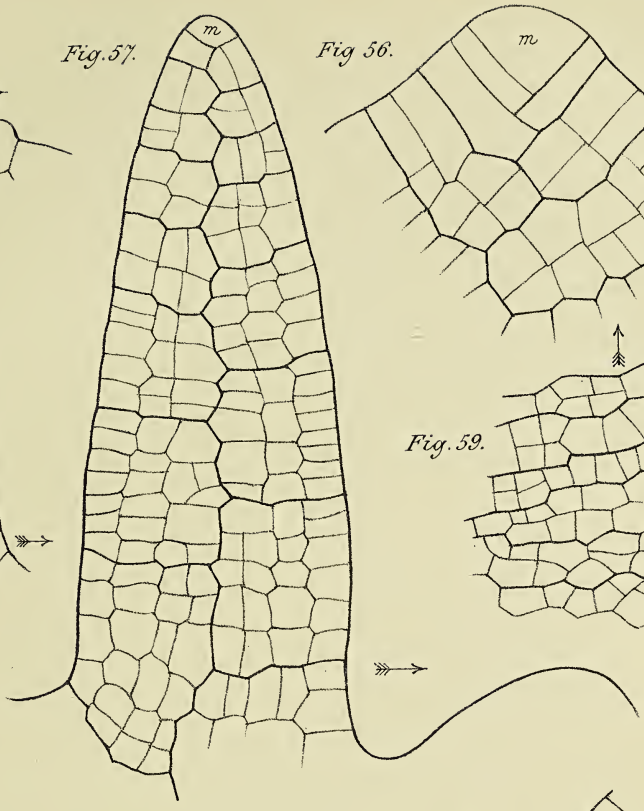

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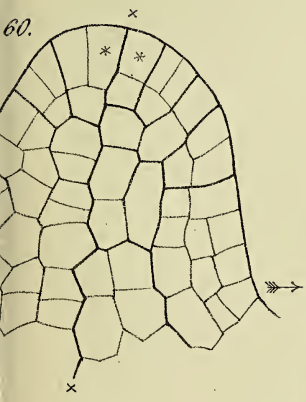

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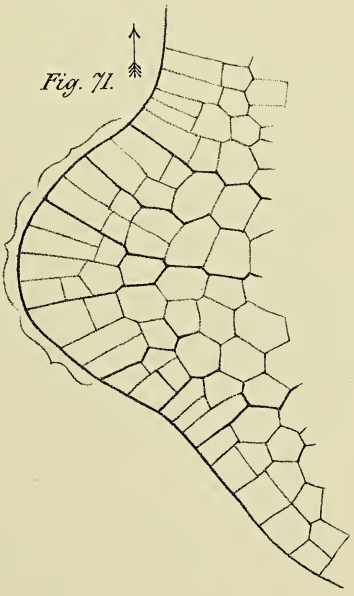
Fig. 71.



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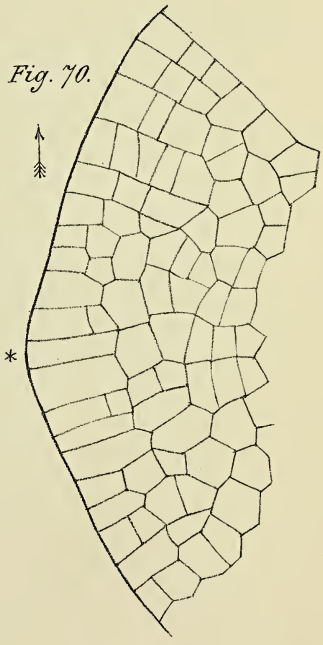

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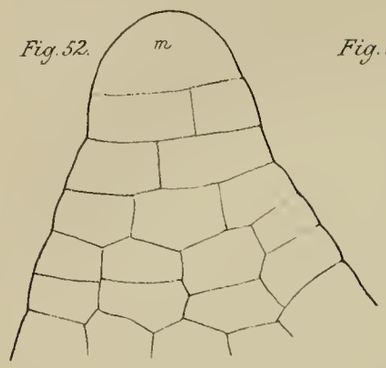

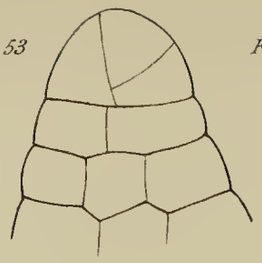

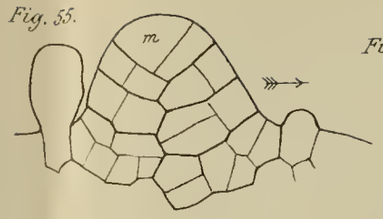

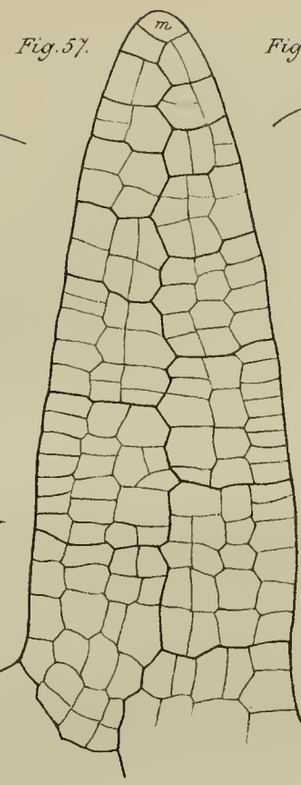

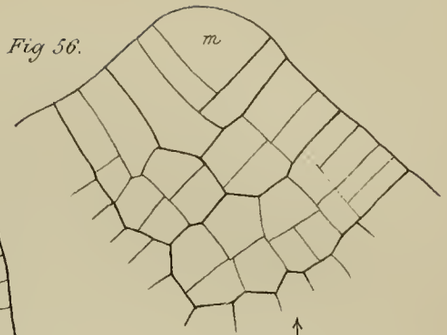

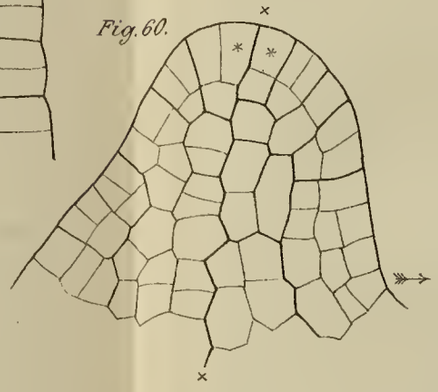

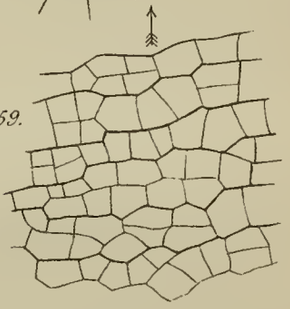

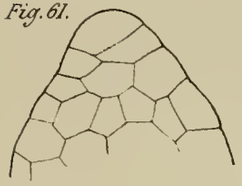

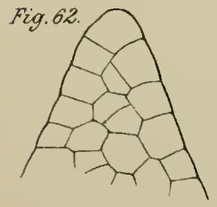

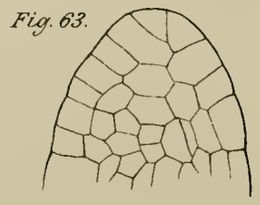

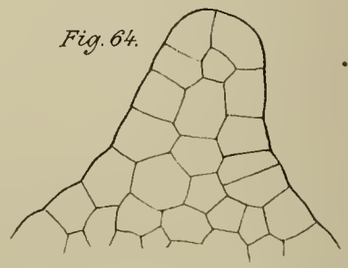

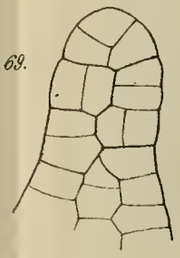

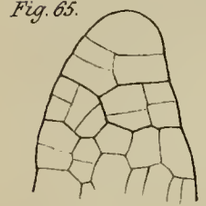

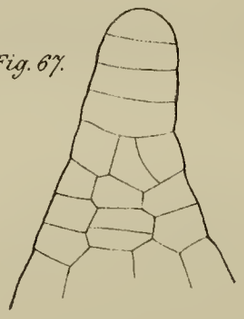

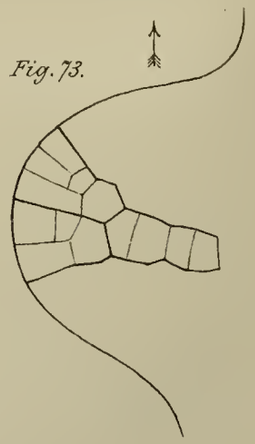

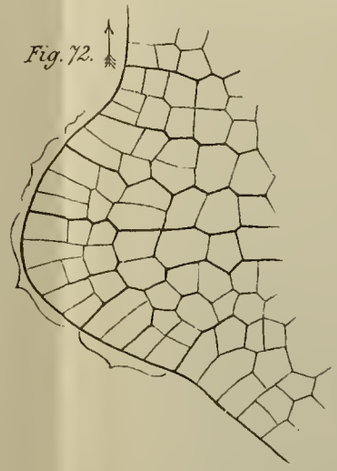

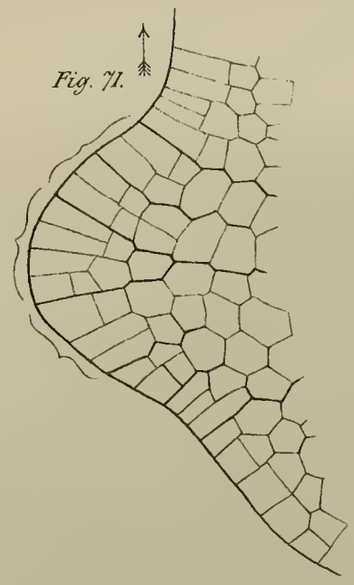

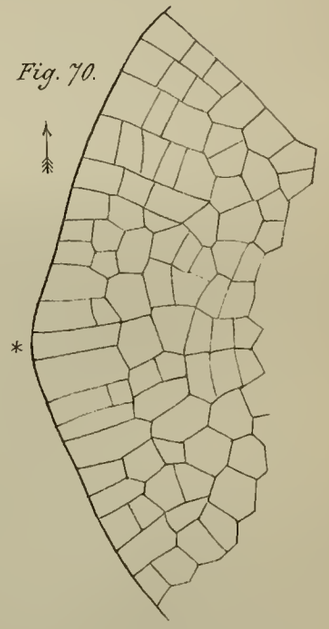

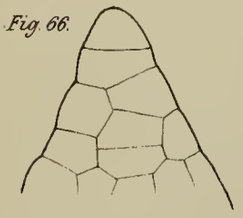

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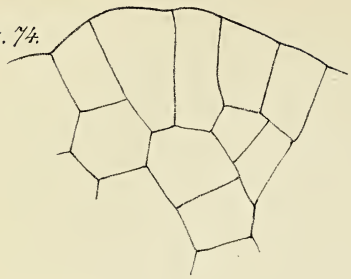

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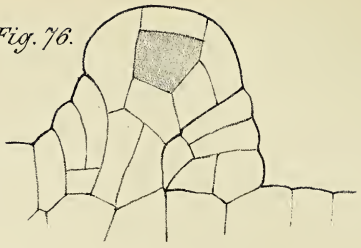

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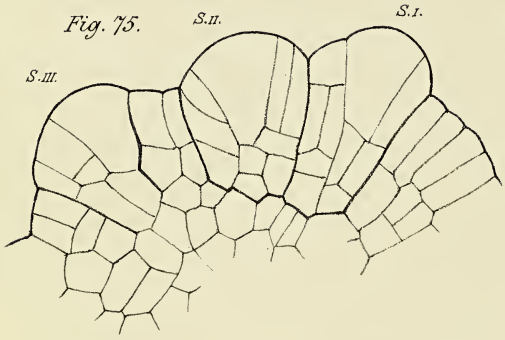

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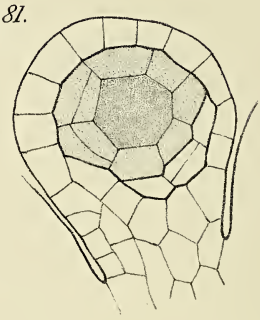

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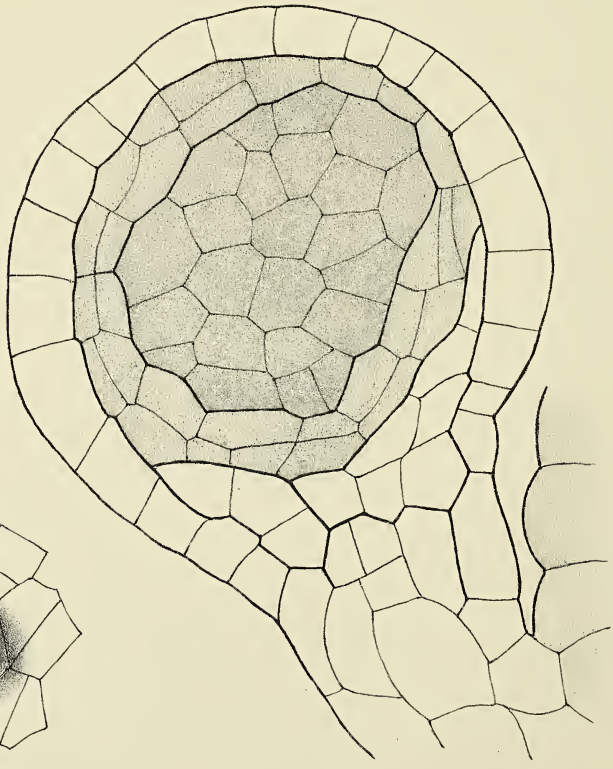

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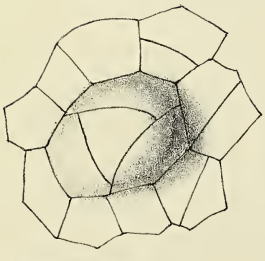

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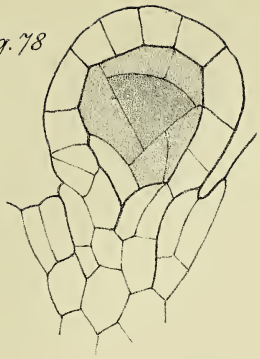

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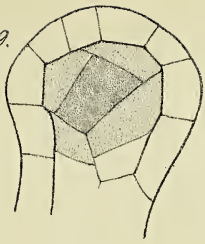

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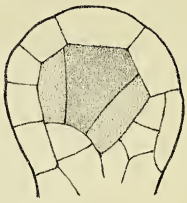

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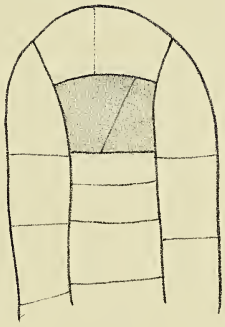

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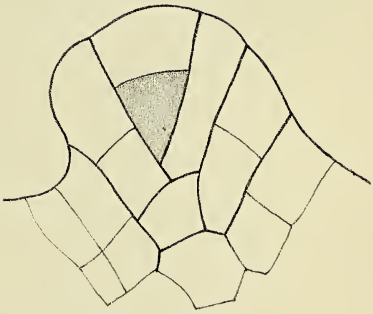

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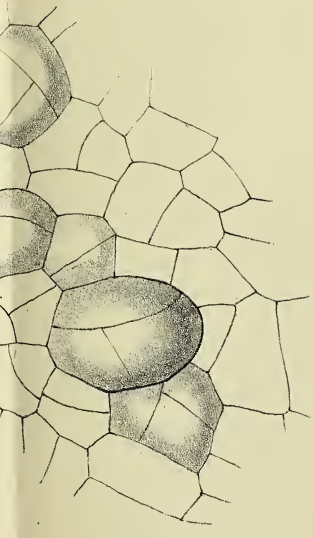

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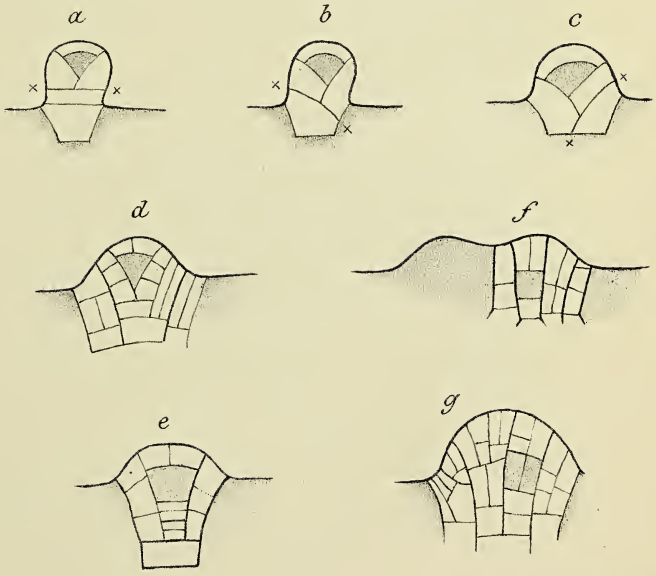

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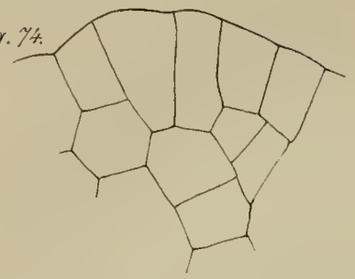

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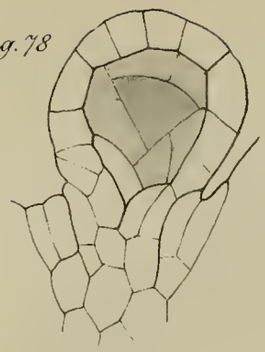

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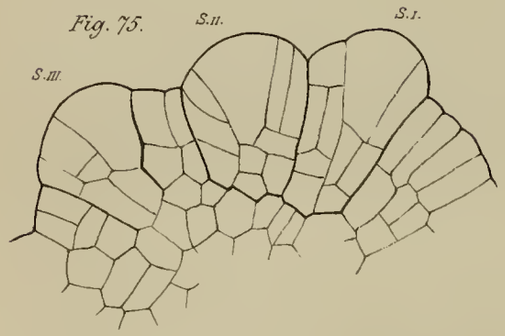

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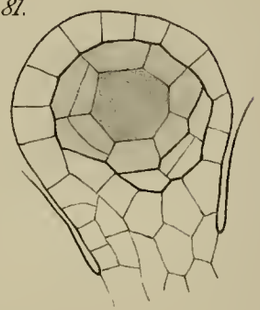

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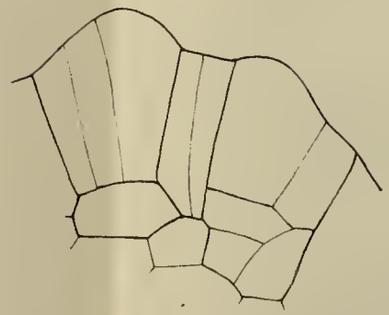

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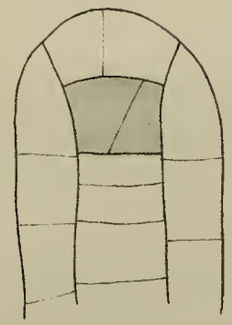

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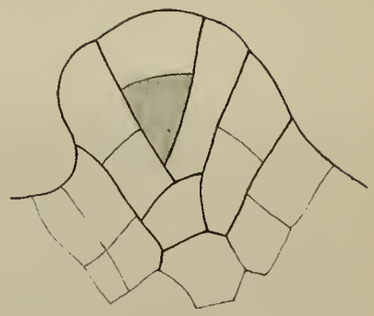

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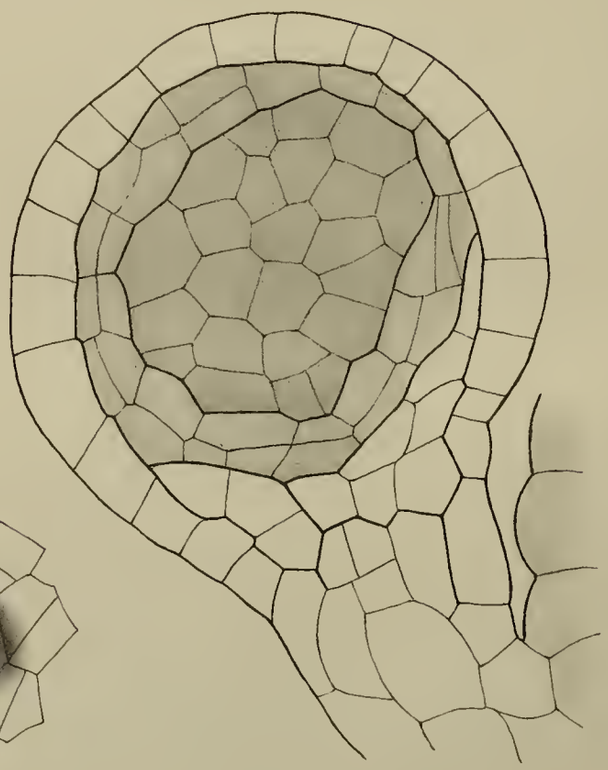

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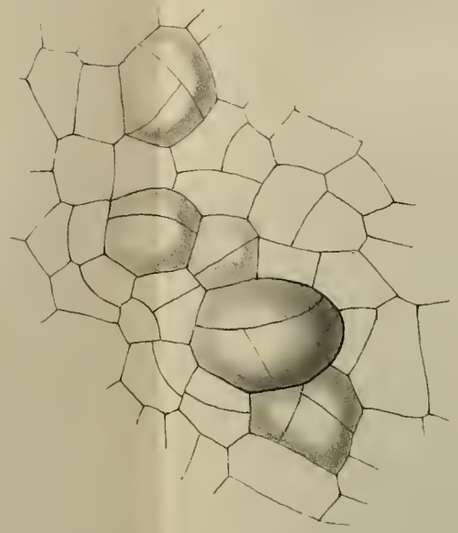

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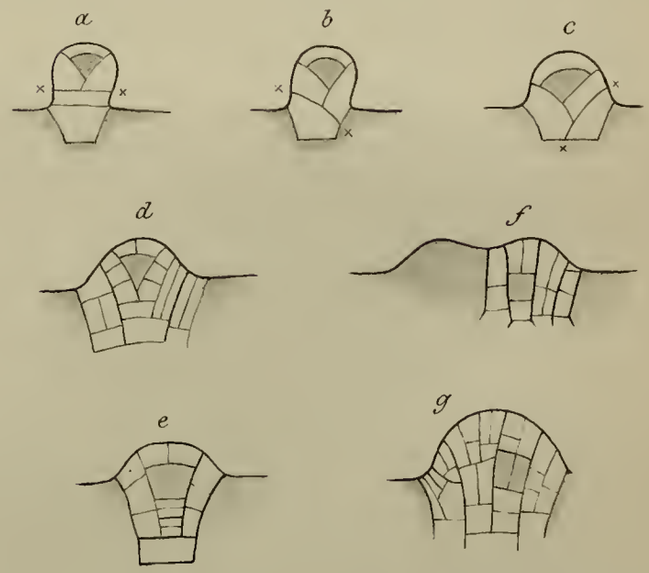
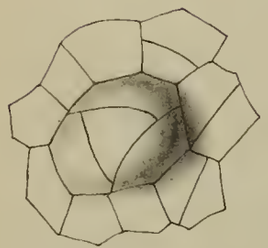


Fig. 85.



F.O. Bower del.

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BOWER.— ON THE MERISTEMS OF FERNS.

Contributions to the Morphology and Physiology of Pulpy Fruits.

BY

J. BRETLAND FARMER, B.A., F.L.S.

With Plates XXV and XXVI.

NOTWITHSTANDING the activity which has, for more than half a century, been manifested in almost all departments of botanical research, the morphology and development of the pulp of succulent fruits still remains an almost untouched field, and the only writer[1] who, so far as I am aware, has dealt especially with this subject, has left very much to be desired as regards the completeness of his results.

Under the term *Pulp*, I include all the tissues, of whatever character, which become succulent in the mature fruit, for it is quite impossible to draw any clear distinction between those usually described as fleshy, as in the apple for instance, and those which are pulpy in the more common acceptation of the term, as in the grape; the one extreme passes quite gradually into the other.

The Botanists of the older school, in describing and classifying the different kinds of fruits, were guided chiefly by the characters presented by mature structures without reference in all cases to the precise origin of the various tissues, and hence it is that the present terminology, which has come down to us with hardly any material alteration, from the days of Mirbel and Jussieu, sometimes fails to convey correct impressions of individual fruits, although, regarded as a whole, its utility

[1] P. Lampe, Zur Kentniss d. Baues ü. d. Entwick. saftiger Früchte; Zeitschr. für Naturw. Halle, Bd. LIX.

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cannot be questioned. Still there does exist a number of fruits which do not correspond in all points to the definitions of any single group, but appear rather to share the peculiarities which characterise more than one class; and others, whilst they conform generally to certain types, are irregular in minor respects. Thus the fruit of *Daphne Mezereon* is commonly described as a berry—a term applied to that class of fruits whose succulent tissue is derived from the pericarp; but in the berry of *Daphne* not only is the pericarp fleshy, but also the outer integument of the seed, whilst the hard seed-coat is formed from the outer layer of cells of the inner integument. Instances of this kind might be multiplied, and in the course of a series of papers which I hope to publish on this subject, I shall have opportunities of describing some of the principal modifications which the various kinds of fruits may present.

It is a fact worthy of notice, that, whilst pulpy fruits are very common in certain natural orders, so much so as to constitute one of the ordinal characters, the morphological nature of the pulp itself may vary considerably within a very narrow circle of affinity. Amongst the British plants, the Caprifoliaceae afford perhaps the best examples of this fact; thus in *Lonicera Periclymenum* not only the pericarp and placenta become fleshy, but also the bracts and axis of the inflorescence; in the nearly allied *L. caprifolium*, however, the succulent tissue is derived from the placenta and pericarp alone. A further modification of the type as represented by *Lonicera* occurs in *Sambucus nigra*, in that here the pulp is reduced to the mesocarp, the internal layers of the pericarp being devoted to the formation of the stony endocarp, and the reduction is carried out with still greater completeness in *Cornus sanguinea*. Similar instances are also furnished by the orders Rosaceae and Urticaceae; but the above is sufficient to indicate the difficulty of arriving at a satisfactory classification of fruits whose chief distinctive feature is subject to so many variations which pass quite gradually one into the other. Of course the significance of

pulp is purely physiological, and hence more than one morphological member may be expected to be called into requisition to furnish it, just as the physiological organs of attachment and absorption may be represented by members other than roots in the true morphological sense of the word; and just as in the latter case, an accurate perception of the morphological nature of the organ which happens to function as a root-like body is indispensable, from a scientific and philosophical standpoint, to the formation of a correct appreciation of the body in question, so also in the case of the class of fruits under discussion: it is impossible that they can be properly understood unless the real nature of the pulp-forming tissue is clearly apprehended.

Besides the extreme case of the Honeysuckle, already mentioned, and the more common forms of berries and drupes, there are some plants, as the Rose and Strawberry, where the entire pulp is derived from the torus; in others the floral envelopes contribute the chief portion, as in *Hippophae* and *Morus*. In *Citrus* again it owes its presence to hairs which spring into the ovarian cavities, and which become distended with liquid. Another, and more irregular source of pulp is found in the aril, which makes its appearance after fertilization in some fruits: an example of this class is afforded by *Taxus*[1]. Even in berries the relative parts played by the placenta and the pericarp show great variety in different plants. Thus in *Vitis* each furnishes about half, in *Solanum Dulcamara* the placenta, and in *Ligustrum vulgare* the pericarp, provides almost the whole pulp.

It is a point of some interest that considerable difference prevails amongst plants as to the time at which the characters which distinguish the mature fruit first come into prominence. Thus in *Hedera Helix* the main features are all apparent before the flower is over, subsequent changes consisting chiefly

[1] There is perhaps some doubt as to whether the structure commonly known as the aril in this plant should be really included under this name; but I have followed the ordinary usage as regards this case.

in extension and growth on the lines already laid down in the bud and flower, except in so far as the cell-secretions are concerned. In *Solanum Dulcamara* the characteristic structure is not reached until the fruit has attained to about one-third of its full size, and in *Rubus fruticosus* the peculiarities of the pulp do not become manifest until the time of maturity is approaching; the 'stone' of this fruit, as in others which possess this structure, is however formed very early, for reasons which will be considered later. It is not always possible to trace the cause of this variation, but there can be little doubt that it is to be sought for in the state of complexity and specialization which is finally reached, for these characters can have been acquired for the most part but comparatively recently; and so in accordance with general principles, they will be proportionately late in their appearance.

To pass on now to the special part of this work, I propose in this paper to deal only with three forms, taken purposely from plants of common occurrence, and which will illustrate some of the varieties which are found in the nature and formation of pulp; later on I shall have opportunity to speak of other anatomical and adaptive characters presented by numerous other forms.

Hedera Helix.—This plant, with its inferior ovary, furnishes an example of a fruit whose pulp is mainly derived from the tissue of the carpels, for though the torus is not altogether without a share in its formation, it plays but a subordinate part in this respect, as will be evident from what follows. If the flower-buds be examined at a time when the inflorescence is just emerging from the scaly bract, it will be seen that the four floral whorls are already laid down, and that the carpels stand at a lower level than the other three whorls. This is due to the fact that they are formed relatively late, and that the external members are early raised up by a zone of growth which is formed below the level of their insertions. The carpels appear as five protuberances within these, and their growth subsequently keeps pace with that of the outer part of the

flower, although, owing to abortion, some of them may remain as arrested forms, the place of these being filled up by the more fortunate survivors. In fact, the whole bud develops in essentially the same way as Goebel[1] has described for the epigynous flowers which he investigated. But from the very first, the tissue of the carpels is clearly marked off from the peripheral cells which owe their presence to the activity of the meristem just referred to, in that in these structures the cell-divisions occur irregularly and without any definite order, except in the few layers destined to form the parchment-like endocarp.

But though cell-division is comparatively irregular in the carpels, it is far otherwise in the four or five peripheral cell-layers which surround them, and which form the cup-like band from which the other floral structures arise. Here the succession of cell-divisions proceeds with great regularity, and chiefly in a direction transverse to the axis of growth, though radial divisions also occur with considerable frequency. So regularly are the transverse divisions formed, that in radial longitudinal sections the cells for a considerable distance can be referred to the original mother-cell (see Pl. XXV, Fig. 2), and form members of a filament somewhat resembling a confervoid alga. Transverse sections show that these filaments are arranged in a very orderly manner as concentric circles, each one cell in thickness (Pl. XXV, Figs. 4, 5). But in spite of the general regularity which the longitudinal and transverse arrangements of the cells exhibit, cases occur by no means unfrequently in which cells, or rather cell-filaments (if the expression may be permitted), do not all divide and grow at the same pace as their neighbours. Sometimes this results in a filament ceasing to elongate, while those in connection with it are still increasing in length, and then the lateral cohesion of the chains of cells with each other is sufficient at times to drag apart the cells of the row which has ceased to divide, and when this takes place the transverse line of

[1] Goebel, Zur Entwick. d. Frunterständ. uchtknoten, in Bot. Zeit. 1886.

separation is almost always at the junction of the ends of two older mother-cells, that is, of cells which have divided a number of times transversely, so as to have given rise to a number of daughter-cells. This fact has some bearing on the problems as to the nature of the causes which effect the separation of cells in general, and in this case the cause is probably to be looked for in the degeneration of the middle lamella, and this explains why the separation commonly occurs between the points of contact of older cells, since such degenerating changes have been longer in operation at these places. In Pl. XXV, Fig. 5, is seen an example of such a separation, and the appearance there represented is highly characteristic of all similar occurrences in this plant. A small drop of gelatinous-looking substance reaches from the tip of one cell to the other, exactly as one would expect on the explanation just advanced. But *Hedera* is not a very suitable object in which to study the phenomena of cell-separation, which is presented in a far clearer manner in *Crataegus Oxyacantha*. If half-ripe fruits of this plant be examined, the cell-walls are seen to be very thick, and even without staining a striking differentiation of the walls into layers is quite obvious. This is of such a nature that the portion of cell-wall which abuts on the cell-contents is clear and distinct, with shallow pits, and resembles that of ordinary parenchymatous elements; but the portion which lies between two contiguous cells is of a brownish colour, and resembles gum in some of its characters. It can hardly be termed mucilaginous, as it scarcely swells at all in water, though potash and strong acids cause a decided increase in bulk to take place. The whole layers of cell-wall are very clearly differentiated by staining with haematoxylin, Hanstein's violet or, best of all, with Schultz's solution. At a somewhat later stage irregular cracks appear in the gum-like middle lamella, and finally intercellular spaces of a large size are formed, and in many cases the slimy substance of the degenerating portion of the wall can be seen stretching across in strands which fuse with the mass lining the spaces (see Pl. XXV, Fig. 17). As degener-

ation proceeds, the cells of the pulp become rounded off, and only remain in contact at points to which the change has not extended. These spots are especially those which appear in younger fruits as pits, and the pit membrane resists the pressures tending to split it apart, and thus are produced the 'glove-finger'-like extensions of the walls of the cells at these places when the rest of the middle lamella around them is swelling in thickness as degeneration proceeds. The presence of these sound parts of the cell-wall is interesting, since, as will be seen later, essentially the same thing occurs in *Hedera*. The (now) free surfaces of the cells which bound the intercellular spaces are seen to be coated with a brown mass, which is somewhat rugose on the surface—exactly the appearance one would expect to find from the manner in which the cells become isolated.

It will be seen that while the final results, namely cell-separation, are the same both in *Hedera* and *Crataegus*, the latter differs from *Hedera* in the great completeness with which the whole process can be followed out. It is probable that the nature of the process is really identical in the two cases, only that in the latter plant the thinness of the walls makes accurate observation difficult. There is, however, in *Hedera* a true mucilaginous degeneration of the cell-wall, which occurs later, and which will be described in its proper place, mention being made of it here for the purpose of avoiding confusion, as its visible occurrence is subsequent to, and could not be traced as a condition of, cell-separation.

But there is a further cause of irregularity in the cell-arrangement of the peripheral layers of the fruit, and this cause consists, not in the arrest, but in the increased activity of growth in individual filaments. Hence, owing to the strong tendency of the other cells to preserve their chain-like arrangement, the growing cell-row pushes its end in between [1] the rows of already formed and still growing rows, and drives them apart. The intruding portions may either be the ends

[1] Cf. Krabbe, Das gleitende Wachsthum b. d. Gewebebildung d. Gefässpflanzen. 1886.

of a cell-chain, or they may arise by the lateral bulging-out of a cell, and the subsequent separation of the protruding portion, by a cell-wall. The new 'apex' just formed then grows independently (see Pl. XXV, Figs. 3, 6, 7) between the cell-rows on all sides of it. It may, however, be urged that the appearance which I have described is simply due to a tangential division extending through a number of cells or through one cell which has then grown *pari passu* with its mother-cells and as a twin filament, but this suggestion is shown to be inadequate by a study of a series of transverse sections in which such an occurrence is taking place (Pl. XXV, Figs. 4, 5). Moreover, I have been able to observe karyokinesis in the terminal cell of one of these intruding rows at an early stage in its formation, and at a time when the surrounding cells exhibited no evidence of continued growth. This observation is not, of course, to be regarded as very weighty by itself, but it is perhaps deserving of mention taken in connection with others, all tending to establish the same conclusion. Another argument in favour of the belief that the filaments are actually intrusive, is to be found in the fact that immediately in front of a cell-row of this character it is very common to find a small triangular splitting, just as would be caused by forcing a wedge of wood into a piece of timber in the direction of the grain (Pl. XXV, Fig. 7).

This intrusion of younger between older cell-rows is by no means restricted to the peripheral layers, it occurs also in the central tissue (Pl. XXV, Fig. 2), which forms the pith in the lower end of the flower, and indeed it is a feature by no means uncommonly to be met with in organs which are growing in any one direction in such a way as to ensure a rapid multiplication of cells in a straight line. Roots, for instance, and some stems, particularly of such plants as Selaginellas, show the phenomenon remarkably clearly. It is true that I have not succeeded in tracing an intercalated row beyond a short distance from its point of origin; this may be partly due to the sinuous course which such rows probably in all cases take, but in any case it is not likely that they reach

to any great distance, as the increasing pressure they would necessarily encounter would certainly prove a serious check to their progress. Still the fact of their occurrence is not without interest in connection with the so-called pseudo-parenchyma of fungi, and other tissues of a similar nature.

At the period when the pedicels of the separate flowers begin to lengthen, the compact mass of tissue of which the carpels are composed suffers a change in appearance, due to the extensive formation of intercellular spaces. Of course the carpels are not composed exclusively of parenchyma, for besides the vascular bundles, there are numerous secretion passages present which are similar to those found in the rest of the plant; since, however, their presence does not materially influence or contribute to the pulp they may be dismissed from further consideration. I have already mentioned the regularity which characterises the cell-divisions taking place in the peripheral layers or rind of the fruit; and it may be regarded as certain that to the rapid radial division, and consequent tangential extension, of this rind is due the early splitting apart of the internal cells of the young ovary. Certainly the cells referred to are subjected to a strain tending to make them occupy a larger space than they normally would do, for besides the fact that cell-multiplication is not very active as yet in this region, growth in size is also very limited, and yet the ovary as a whole is increasing very largely in bulk. The cellular tissue splits up, then, to allow of this increase, but it is rather a passive, than an active process like that in *Crataegus*, and the cell-walls are still very thin, no clear middle lamella being visible until specially looked for, nor have I as yet succeeded in tracing any connection between the splitting and a degeneration of the cell-wall in this inner mass of cells. But the walls are so exceedingly thin that it might easily escape even careful observation, and the formation of mucilage already hinted at, and which will shortly be described, renders it quite probable that such a connection does exist. The cells which eventually separate do not however become completely isolated, but remain united with each other by their ends, so as to form

contorted and convoluted ribands of one or more cells in thickness, which anastomose freely with each other, while their free ends project into the meshes of the rude mesh-work of intercellular spaces, of which they themselves form the boundaries.

The cell-rows which together constitute the rind remain united chiefly by their radial walls, and separation, when it occurs, is mainly restricted to the tangential walls. In the latter may be seen indications of the same process which I have described for *Crataegus*, and also for those cell-rows of the rind which are separating, as seen in longitudinal sections of flowers and young fruits. A well-developed middle lamella is commonly traceable before the commencement of the changes which ultimately result in the separation of the cell-rows (Pl. XXV, Fig. 10).

After the flower has withered, rapid multiplication of cells takes places in the vicinity of the ovaries whose ovules have been fertilized, and this is especially noticeable in the lax tissue of the carpels; any one cell may elongate in almost any direction, and then by division give rise to the rudiment of a fresh riband of cells, which grows in the meshes formed by the older cells. Sometimes single cells divide into four daughter-cells, each of which becomes a new centre of cell-formation, and indeed the whole process reminds one somewhat of the budding of yeast. Beautiful karyokinetic figures are seen during the process, showing the activity with which division is proceeding, and in this way the interior of the fruit again becomes more firm as the large production of fresh tissue takes place.

I have said nothing hitherto of the formation of the endocarp in this fruit. It is due to the three or four layers of cells which line the ovarian cavities, but it is very slightly developed, and it is perhaps best left for consideration in connection with other forms in which a greater degree of completeness is reached.

If the young fruits gathered about the end of January be examined, the cell-walls which bound the intercellular

spaces are found to be covered with a substance of mucilaginous or gelatinous nature, and which is obviously related to the cell-wall itself. The substance is very transparent and homogeneous, and may readily escape observation altogether unless staining reagents are employed, and these have to be used with some care, because if water be applied to the sections previous to staining, it rapidly swells up and disappears. Haematoxylin, Bismarck brown, and Hanstein's violet all gave fair results, but the two former reagents were by far the most satisfactory. If the section of material which has been preserved in alcohol be rapidly washed with water, and then stained with Kleinenberg's haematoxylin, the mucilage appears as a glairy substance lying in the intercellular spaces and around the edges of the section; but if the sections are stained at once without rinsing with water the mucilage is seen in its unswollen condition. In this state (e.g. after staining) it refuses to swell up, owing perhaps to the alum in the reagent, and the same is true of chromic acid material.

It is found either lining the cell-wall or aggregated in little drops, and in the latter state the drops most frequently occur at places where two cell-walls meet. As the fruit grows older the mucilage becomes more and more apparent, and when sections of alcohol material which is almost ripe are placed in water, a very rapid separation of the cell-layers is seen to take place, due to the expansion and swelling of the intercellular mucilage. It is best studied in alcohol material, since if fresh fruits are cut the protoplasm also issues from the cut cells and interferes with the observations, as it is itself of a glairy consistence, and is so abundant as to mask everything else in sections of younger fruits. It appeared possible that the entire mucilage might be derived from this source, but the contracted primordial utricles, which are present in alcohol material, showed no trace of the substance in their interior, nor was it present in the space left between them and their cell-walls. Still, the extremely sharp line of demarcation which exists between the non-swollen part of the cell-wall and its mucilaginous investment gives at first some support to the idea that

the latter might be of the nature of a secretion, which spreads over the free portions of the cell-walls which line the intercellular spaces. Reference, however, to *Crataegus* and other similar forms shows that this point has but little weight, and besides this, it is not likely that cells engaged in rapidly dividing would be also employed at the same time in actively secreting mucilage. Thus, although the actual steps resulting in its formation are difficult to follow, there can remain but little room for doubt that the substance in question owes its origin to degenerative changes which are going on in the outer layers of the cell-walls, and which only become evident at a period subsequent to the splitting apart of the cells, which results in the formation of the intercellular spaces referred to. And indeed it has already been pointed out that the cells of the interior of the fruit are obliged to split, in order to admit of the radial extension of the whole, since the peripheral cells divide, at first, in such a way as necessitates either such an expansion, or a throwing of the surface into folds, and in this way it is possible that the result may become manifest before the cause which effected it.

Whilst the mucilage is apparent at an early period it becomes far more pronounced as the time of maturity draws near. The number of cells of which the pulp is composed is at this time very large, but the riband-like arrangement is still easily discernible, especially near the periphery; in consequence, however, of the increase in the absolute size of the cells in the internal part of the fruit, the bands become forced into close juxtaposition, and the intercellular spaces form a proportionately smaller part of the entire volume of the fruit. Hence in sections taken through mature specimens the process of swelling can be readily followed out, as the addition of water to the preparation effects a great displacement of the cell-ribands, which were originally almost in contact.

The cell-contents do not present any features of striking interest as long as the fruit continues to grow in size. Chlorophyll is present, especially in the peripheral layers of cells, and

starch is also in some cases distinguishable, though only in very small quantities. Crystals of oxalate of lime are not uncommon, especially near the vascular bundles; but the most interesting of the cell-contents is the oil which is present in minute quantities in the protoplasm of all the cells. This substance is often only detected with difficulty until the fruit is ripe, but careful staining, especially with osmic acid, generally succeeds in making it apparent. As the fruits ripen, on the other hand, the volume of oil in the cells increases very largely; it forms aggregates of spherical drops of a considerable size, which are surrounded by a delicate pellicle of protoplasm, which serves to keep the several drops asunder. When it is being secreted at this late stage of the development of the fruit, it is seen to appear in the first instance as a number of excessively small brightly refracting globules, which are embedded in the substance [1] of the comparatively thin primordial utricle. The globules increase rapidly in size and run together so as to form larger and larger drops, though each drop is, at least temporarily, provided with a membrane which serves to separate it from the rest in its immediate vicinity. This limiting membrane must disappear between the points of contact of drops about to fuse, in much the same way as two soap bubbles behave when placed in such a position that their cavities are about to unite, for, although I have not actually seen the process in operation, it must occur, since the number of drops grow less as the actual size gets larger. But besides the increase in size caused by running together of the drops, there is the active process of secretion going on in the protoplasm, and by virtue of which its own substance is gradually used up. The larger drops now project into the cell vacuole and soon fill it, while the protoplasm only remains as a thin layer lining the cell-wall, and the now large oil drops. Addition of potash, especially on warming, causes the oil to run into

[1] Cf. Wakker, Studien ü. d. Inhaltskörper d. Pflanzenzelle; Prings. Jabhrb. XIX. Bd. 1888. I have not been able to trace any structures resembling elaioplasts in *Hedera*, but it is perhaps a significant fact that the chlorophyll-granules are still intact during the oil-secretion.

one or two large globules, by effecting the disappearance of the membrane; no saponification takes place at all, the oil is quite unaltered by potash, even when treated with it for a considerable time. It is, however, easily dissolved by ether, chloroform, or turpentine, and from these solutions it may readily be recovered by distillation. Osmic acid stains it quickly, and proved a most useful reagent in aiding the watching of its formation, but fair results were also obtained by lengthy treatment with solutions of iodine.

The oil-forming tissue is found chiefly in the inner part of the fruit. The cells of the rind, though they contained it in small quantities, are for the most part filled with the red sap to which so many dark-coloured fruits owe their characteristic appearance. Still, these may also be regarded as forming, together with the carpels, the pulp of the fruit which is thus derived from the whole mass of the ovary, with the exception of the few cells which are devoted to form the soft parchment-like endocarp. I do not propose to deal with this structure here, but to reserve it until it is met with in a better developed form in other types. Still, although it is feebly represented, it has as much claim to regard, from a taxonomic standpoint, as that in *Sambucus* or *Prunus*; and I think it is a pity that all these fruits are not included under the common term drupe, instead of artificially restricting this term to a one-seeded form. For they all agree in the essential feature of the endocarp, and fall quite naturally into the same category, whereas under the present system both *Hedera* and *Sambucus* are removed from their obvious alliance with forms like *Prunus*, and placed in the same class with *Vitis* and *Daphne Mezereon*.

Rubus fruticosus.—This fruit gives us an example of the drupaceous type, in which a portion of the pericarp only is devoted to the formation of pulp, the remainder undergoing modification to enable it to meet other and special requirements. If the walls of the ovaries are examined in the young state, shortly before the unfolding of the flower-bud, the cells of the middle and outer regions are seen to be arranged in irregular radial rows, each containing about eight to ten cells.

Externally these are bounded by the epidermis, but internally they pass into an inner zone of tissue, which lines the cavity of the ovary, and which consists of very small cells which form a somewhat misty-looking layer. It is from the last-mentioned tissue that the stony endocarp is formed which renders the examination of all but very immature fruits a matter of considerable difficulty. The number of cells does not increase greatly, the divisions which do occur are mainly transverse to the long axis of the fruit; tangential divisions are very rare, except in the peripheral cells, which ultimately form the epicarp, although even here they are by no means of common occurrence.

As the drupes increase in size after the flower has withered, they are unable to expand equally in all directions owing to the mutual pressure consequent on their crowded condition, and hence each is broadest at its upper portion (Pl. XXV, Fig. 20). When differentiation begins in the pericarp, those cells which finally give rise to the endocarp are the first to become specialized. These cells consist of fibres so elongated that a chain of such fibres running round the fruit cavity resembles a segmented ring or hoop. Owing to the regularity with which the cells fit into one another, this appearance is rendered most strikingly prominent, and the whole of the interior of the ovary appears to be bounded by these 'rings,' which run in a transverse direction round it. Only a part of the endocarp, however, forms these transversal rings, the rest consists of fibres, also regularly arranged, but whose longest axis runs in a direction at right angles to that of the cells just described. The result of this arrangement is that the ovarian cavity is protected by a band of tissue, of which one half is fitted to stand strains and stresses in one direction, while the other half is equally well capable of resisting similar strains and stresses in a direction at right angles with the first. The regularity of the two systems is somewhat broken by subsequent changes due to growth, but the general formation is sufficiently obvious even in ripe fruits. The endocarp, when differentiated, rapidly increases in thickness in the way I have

already described for *Sambucus nigra*[1], only that here the 'slipping' takes place to a far greater extent, and the later addition, so remarkable in *Sambucus*, is entirely wanting in *Rubus*. Lignification sets in very early in the cells of the endocarp, and results in the conversion of the entire tissue into the well-known hard shell which encloses the seed of so many drupes. Markings of a pitted character may be detected in these fibres, whose walls thicken to such a degree as to almost obliterate the cell-lumen; but as we shall see later, many other fruits exhibit these markings in a state of much greater perfection.

At a stage subsequent to that at which the endocarp has become clearly recognisable, the character of the cells at the periphery of the fruit begins to change and the limits of the epicarp are defined. I have already mentioned the fact that exclusive of the endocarp, the cells are roughly arranged in radial rows, each containing about eight to ten cells. The outer four or five of these become gradually flattened radially, and consequently extended tangentially, whilst their walls also are thickened as the process of distortion takes place. The cells which are thus displaced from their originally regular position, form an interlocking mass of a very tough texture, and this mass represents the removeable skin which encloses the softer portions of the fruit. Internally the cells pass by a somewhat sudden transition into the pulp, which must now be considered. At the inner boundary of the epicarp, which consists, as I have said, of flattened elements, there is a layer of cells which are of an approximately isodiametric shape, and whose walls, unlike those of the cells of the epicarp, are exceedingly thin. This layer forms the outer boundary of the mesocarp or pulp proper.

As would be expected from the conditions under which the separate drupelets are placed, the mesocarp does not surround the endocarp as a layer of equal thickness throughout, but is developed to the greatest extent on the free portions where

[1] Ann. Bot. vol. ii. p. 389.

the pressure caused by mutual contact does not exist. The cells, two or three deep, which lie internally to the thin-walled elements above mentioned, undergo a remarkable change of shape shortly before the fruit reaches maturity. They suffer an enormous extension in the radial direction, so much so that they can be compared to nothing so well as to cylinders whose ends are rounded. Intercellular spaces make their appearance during this alteration which separates one cylindrical row from the others around it, and serve to bring out the striking individuality of these cells into yet sharper relief. It is owing to the presence of these cells, whose thin walls bear so small a proportion to the bulk of fluid which they contain, that the interior of the fruit appears to be filled with nothing but juice. If the walls had been a little thicker, and the cells greater in number and consequently smaller, a fruit would have been produced which would have occupied a position intermediate between such forms as the blackberry and the more fleshy types which are represented by members of the other end of the series.

The cylindrical cells pass quite abruptly into a tissue composed of small and crowded cells, which forms an ill-defined layer outside the endocarp. It is not easy to say whether they should also be referred to the mesocarp, and yet they certainly do not belong to the endocarp, but they form rather a neutral ground between these layers, and serve merely to establish continuity between the inner and middle zones of the fruit.

It is manifest that a considerable difference exists, both as regards the origin and mode of development of the pulp in the two cases we have hitherto considered; for whilst in *Heaera*, in addition to the carpels, the raised up portion of the torus also enters in part into its formation, in *Rubus* the whole is formed from a limited portion of the tissue of the carpels. Again, whilst in *Hedera* all the characters, apart from those which are the result of secretional activity, could be predicted from the structure of the bud, in *Rubus* it is not until the approach of maturity that the most striking features of the fruit

become visible. A further point worthy of note is the difference in the endocarp of the two plants, and while this perhaps finds its explanation partly in the fact that the ripe seeds of the blackberry require more protection than those of the ivy, I think this is by no means the whole explanation. If the mode of growth which prevails in the two cases be compared, it will be seen that they are fundamentally different. In *Rubus* the peripheral cells do not divide, or only to a slight extent, but suffer flattening by the expansion of the cells interior to them. The effect of this is of course to produce considerable pressure on the interior cells, and it is conceivable that this pressure might exert a prejudicial influence upon the delicate ovule which, but for the presence of the resistent endocarp, would be exposed to the full influence of this force of compression. As it is, however, owing to the remarkable manner in which growth takes place in the cells of the endocarp, the effect of such a pressure on the ovule is entirely obviated, and it is able to develop in a free and unconstrained manner. In *Hedera*, on the other hand, the cells of the rind are rapidly dividing, and, as we have seen, the internal tissue is unable to keep pace with the extension, and its cells are rent apart. Consequently the ovules in this plant are not in the least subjected to the action of a force like that obtaining in *Rubus*, and hence the early development of a means of protection would be superfluous. That the tensions and pressures really exist may be easily shown by cutting the fruit across and noticing the way in which curvatures take place. *Sambucus nigra* affords a particularly good example of a fruit whose ovule would require protection, since if a longitudinal section of moderate thickness be cut through the fruit when about half ripe, and if then the hoop which is formed by the endocarp be divided at one end, the free ends thus formed at once cross over each other and reduce the size of the fruit cavity.

Rubus Idaeus presents essentially the same structure as *R. fruticosus*, except that in this plant the epidermal cells grow out into long hairs.

Solanum Dulcamara.—In the fruit of this plant we meet with a case in which the pulp owes its origin to two sources, being derived partly from the wall of the superior ovary, and partly from the tissue of the placenta. The carpels at the time of flowering are somewhat thin structures, containing a number of vascular bundles which run at a distance of about eight cells from the epidermis, and even at this period there is a difference perceptible between the cells which lie outside, and those which lie inside, the zone of vascular bundles. The former already show a flattening of their cavities like those which correspond to them in *Rubus*, and this appearance is accompanied by a slight thickening of their walls. The cells of the interior, on the other hand, are fairly isodiametric and thin-walled; they are much distended with cell-sap, and their protoplasmic contents become reduced to a thin primordial utricle, as may be easily shown by plasmolysing. Those cells which immediately bound the cavities of the ovaries are somewhat smaller than the rest, but they show no marked irregularity of size.

At the flowering time, the ovules stand out from the placenta into the cavities of the bilocular ovary and do not touch the carpel-walls, but if fertilization is effected this state of things is soon altered. Radial and tangential divisions arise in the layers of cells lying beneath the inner limiting layer (epidermis) of the carpels, and this process causes an ingrowth of the tissue of these bodies into the space left between the ovules. At the same time the cells of the placenta also multiply and grow larger, though the limit of possible expansion of this structure is of course determined by the size of the fruit-cavities. The placenta, however, takes advantage of all the spare room left between the ovules, and by growing out between them, causes them to appear as if they were sunk in its substance (Pl. XXVI, Fig. 30). Those processes grow outwards, enclosing the ovules, until they finally meet with the similar ingrowths of the carpels, which likewise penetrate between the separate ovules. The two surfaces then become pressed together, and the line of demarcation between them is

gradually obliterated, and complete union takes place. In this way the ovules become entirely enclosed in the pulpy tissue, even long before the fruit is ripe, and it is impossible to distinguish that portion whose origin is carpellary from that which is derived from the placenta. The changes which take place in the outer cells of the pericarp, and which result in the formation of an epicarp, have already been adverted to, and need not be further described, as they are essentially similar to those occurring in *Rubus*, except that here the epicarp is somewhat thicker, and separates with greater ease from the inner tissues.

Whilst the changes above detailed are proceeding, modification is going on in the outermost layer of the ovular integument, which results in the formation of a protective shell, which takes the place of the endocarp in other fruits. The thickening substance, which soon becomes strongly lignified, is deposited on the inner or central wall, and extends partially up the lateral or radial ones, but, as in many other cases, it is not complete, and hence a section of the young seed shows these walls as spike-like projections which terminate in thin membranes. The outer, or peripheral, wall is not thickened at all, but its more external layers undergo mucilaginous change (Pl. XXVI, Figs. 31, 32) at a very early period. This mucilage may perhaps be regarded as part of the pulp, as it fills the interspaces left between the ovules and the surrounding tissues as a somewhat viscous mass. It is of extremely common occurrence in fruits, and owes its origin to the most varied sources; we have seen it in *Hedera*, and in *Ribes* it is also met with, being derived from the placental cells; and besides these instances it occurs in a great number of fruits, as *Linum* (where it is produced from the seed-coat as in *Solanum*), whose ovaries do not become pulpy at all.

As the fruit ripens the green colour changes to the well-known bright red, so characteristic of the berries when mature; the change is due to the appearance of a great number of orange-red chromoplastids, which are, in part at least, derived

from the chlorophyll granules [1], and fruits such as those of the Bittersweet afford fine examples for studying the development of these structures. Unfortunately most of my material was preserved in alcohol, so that I was unable to follow all the steps of the process, which can of course only be done in perfectly fresh specimens. As the colour of the ripening fruit begins to change, the starch, which previously filled the cells, slowly begins to disappear, and no trace of this substance can be detected at maturity, its place being taken by sugar, which is dissolved in the cell-sap.

I cannot bring this paper to a close without recording my warmest thanks to Professor Bayley Balfour, at whose suggestion this investigation was undertaken, for the kindly help and advice which he has given me during its progress.

[1] See Schimper, Ueber die Entw. d. Chlorophyllkörner u. Farbkörper, Bot. Zeit. 1883; also in Pringsheim's Jahrb. Bd. xvi. p. 131.

EXPLANATION OF FIGURES IN PLATES XXV AND XXVI.

Illustrating Mr. Farmer's paper on the Morphology and Physiology of Pulpy Fruits.

Figs. 1–14. *Hedera Helix.*

Fig. 1. Longitudinal section through young bud. The shaded part represents the tissue of the carpel. *v*, vascular bundle.

Fig. 2. Longitudinal section through elongating portion of pith, just below carpels, shows two cell rows pushed apart by intruding filament, *F.*

Fig. 3. Longitudinal section of part of the rind: two cell rows growing past each other.

Figs. 4, 5. Successive sections (transverse) through young fruit rind. *aa*, sections through the same intruding filament.

Figs. 6, 7. Longitudinal section through rind. *E*, epidermis.

Fig. 8. Transverse section through carpellary portion of half-ripe fruit. *m*, intercellular mucilage.

Figs. 9, 10, 11. Transverse sections through parts of older fruits (Haematoxylin).

Figs. 12, 13, 14. Cells with oil contents from almost ripe fruits.

Figs. 15–18. *Crataegus Oxyacantha.* Middle lamella, coloured yellow.

Fig. 15. Transverse section of $\frac{1}{3}$-ripe mesocarp. The well-differentiated middle lamella as seen when mounted in water.

Fig. 16. The same in potash.

Figs. 17, 18. Somewhat older, mounted in Schultz solution.

Figs. 19–23. *Rubus fruticosus.*

Fig. 19. Diagrammatic transverse section, young fruit, showing layers of the endocarp.

Fig. 20. Same in longitudinal section.

Fig. 21. Transverse section of ovary in the bud.

Fig. 22. Same sometime after flowering.

Fig. 23. Same when almost ripe.

Figs. 24–32. *Solanum Dulcamara.*

Fig. 24. Longitudinal section, ovary in flower.

Fig. 25. Same shortly after flower has withered.

Fig. 26. Transverse section of ovary in same style as in Fig. 25.

Fig. 27. Transverse section, young epicarp.

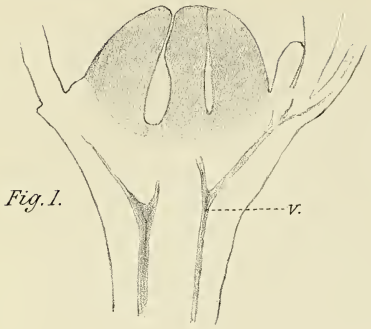
Fig. 28. The same much more advanced, part of the mesocarp also shown. *E* = epidermis.

Fig. 29. Transverse section of inner portion of pericarp in same stage as Fig. 25; some of the cells are dividing tangentially, to form the inner ovular protuberances. *I. E.* inner epidermis or limiting layer.

Fig. 30. Shows the pericarp (*Pe*), meeting placental (*Pl*) outgrowth, round two ovules (*o*).

Fig. 31. Transverse section through ovule, showing mucilaginous layer (*m*).

Fig. 32. Mucilaginous layer (*m*) in later stage; *s*, the thickening seed-coat.



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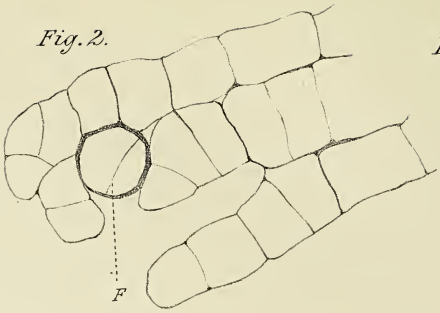

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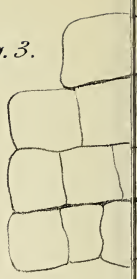

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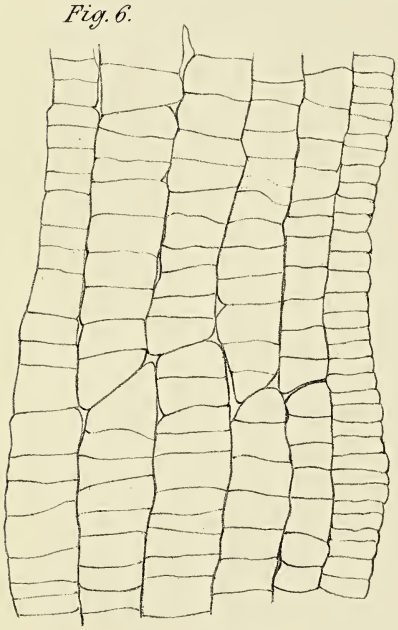

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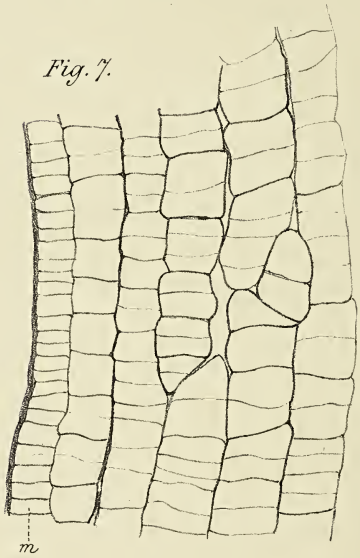

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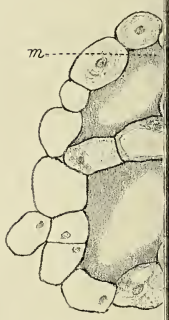

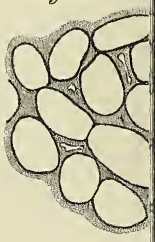

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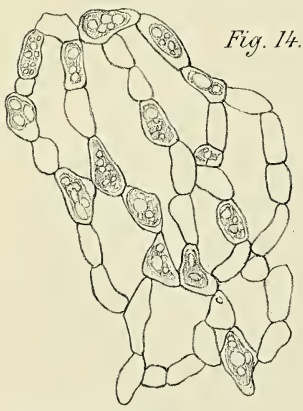

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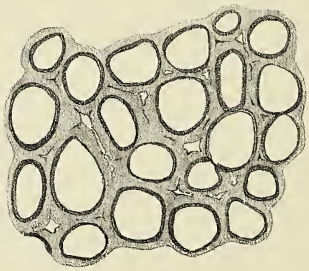

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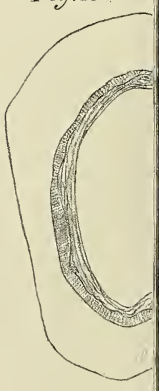

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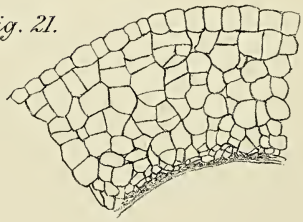

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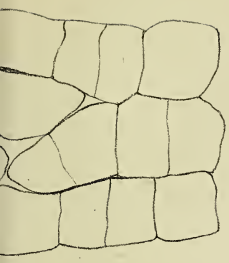

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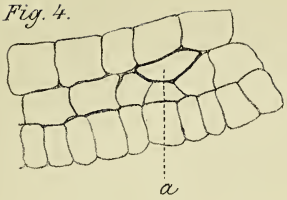

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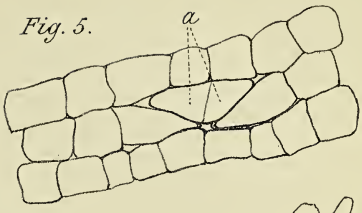

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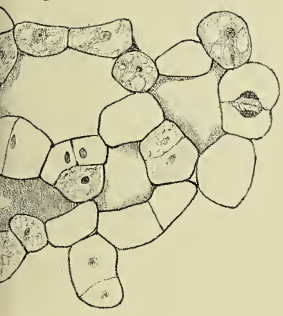

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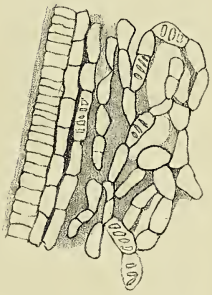

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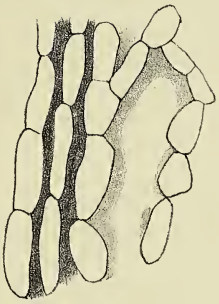

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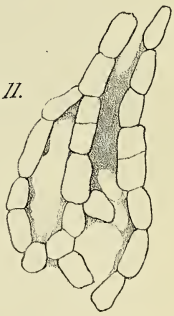

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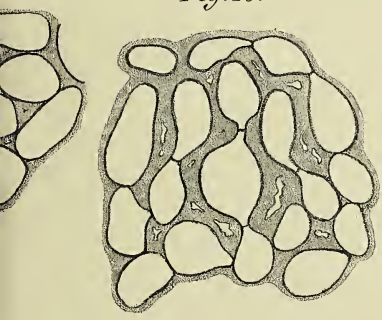

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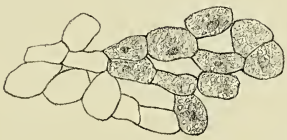

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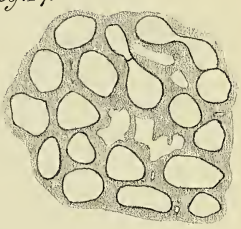

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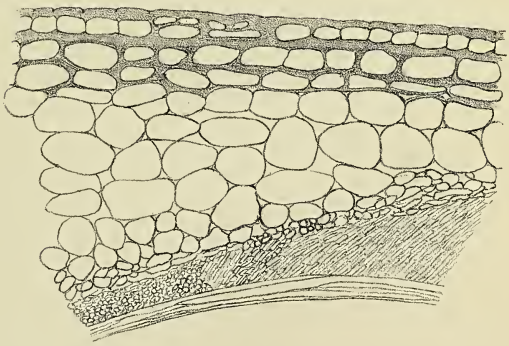

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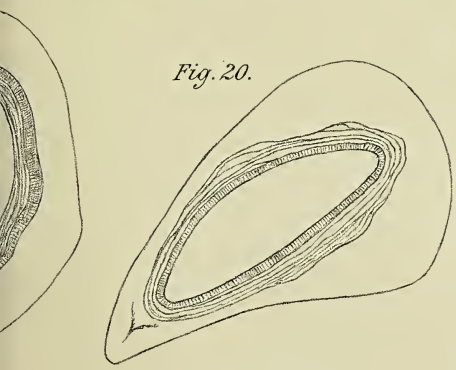

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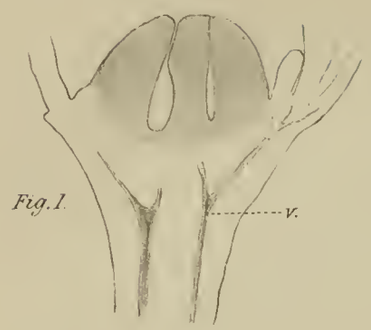

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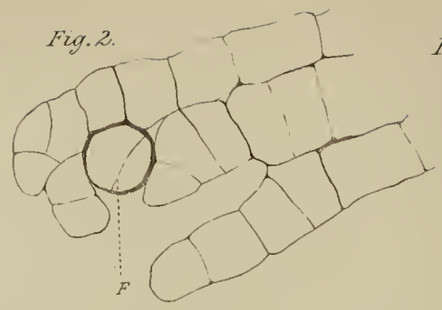

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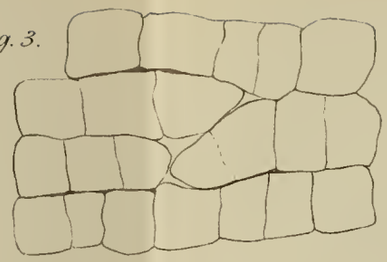

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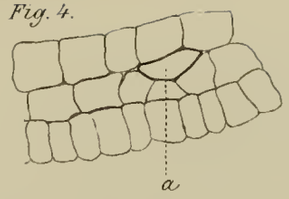

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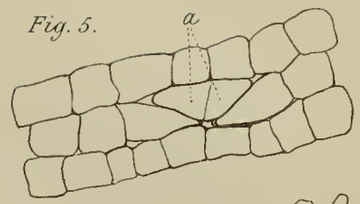

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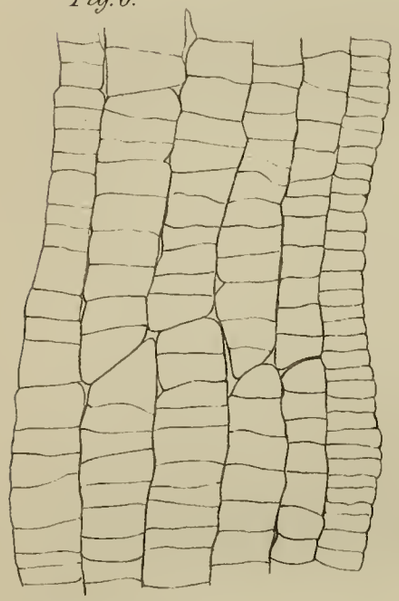

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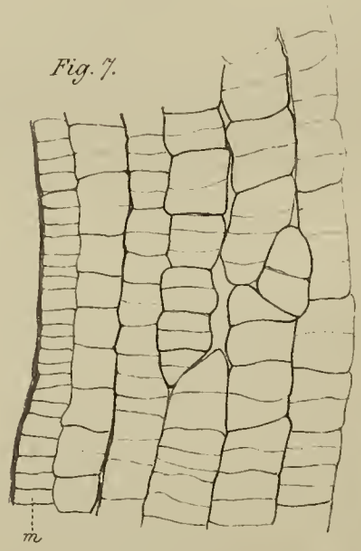

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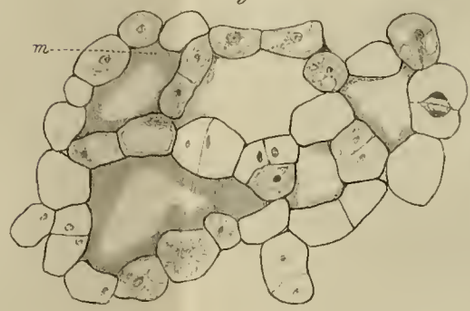

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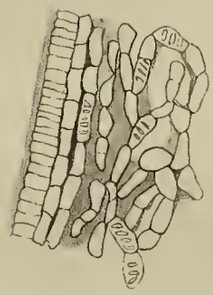

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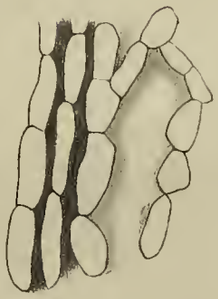

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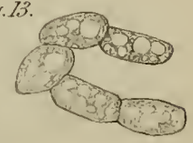

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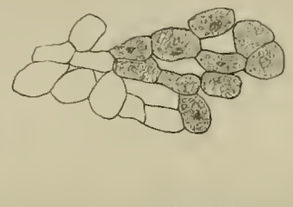

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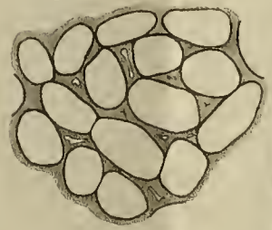

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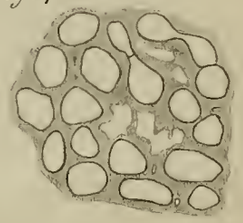

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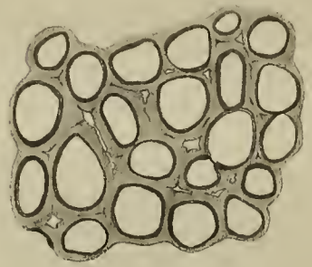

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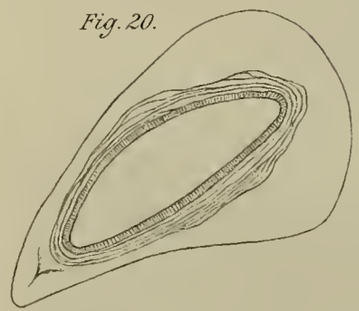

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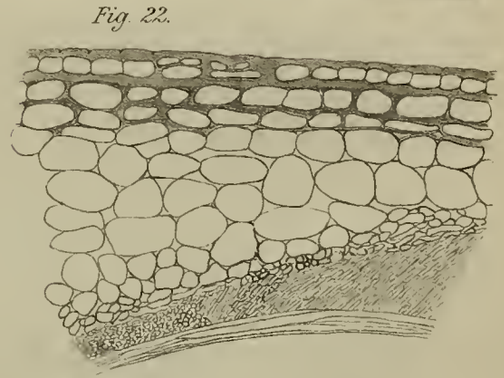

Fig. 22.

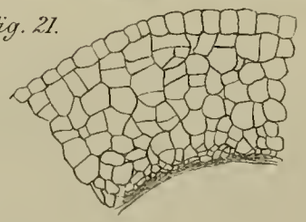

Fig. 21.

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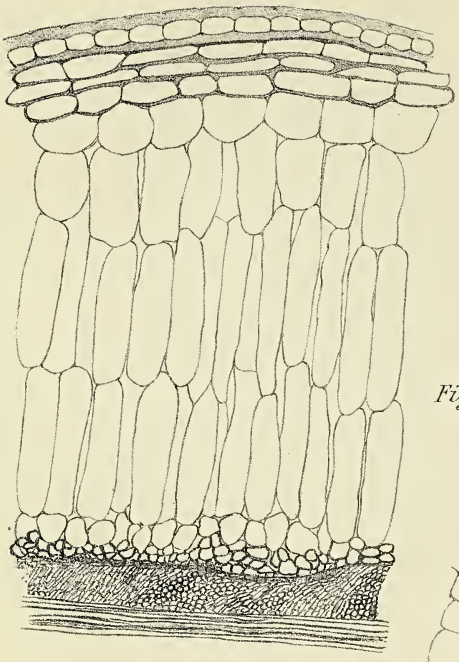

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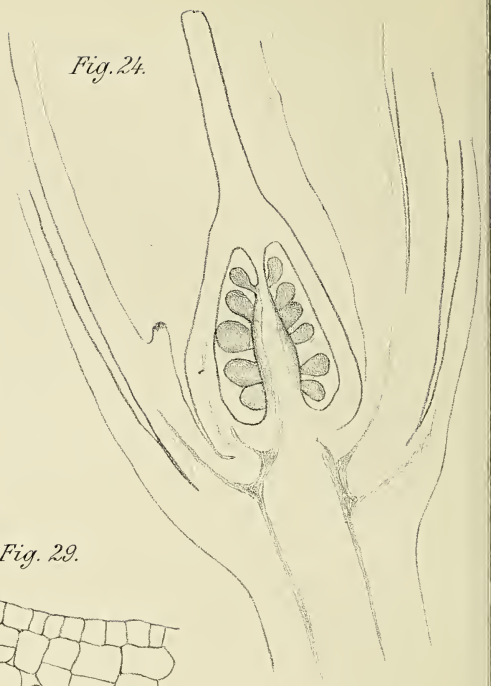

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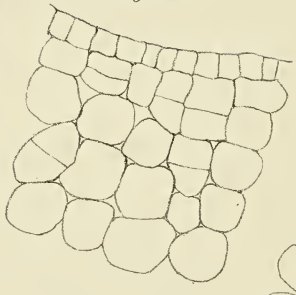

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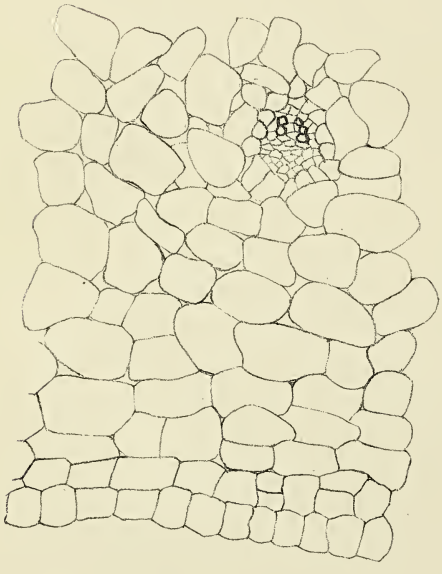

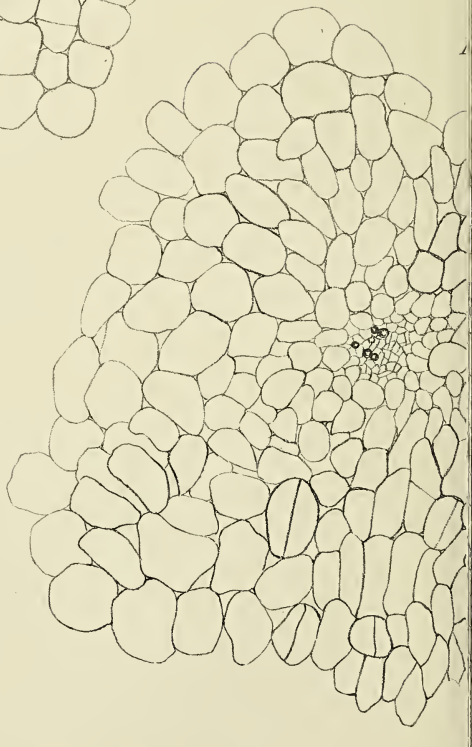

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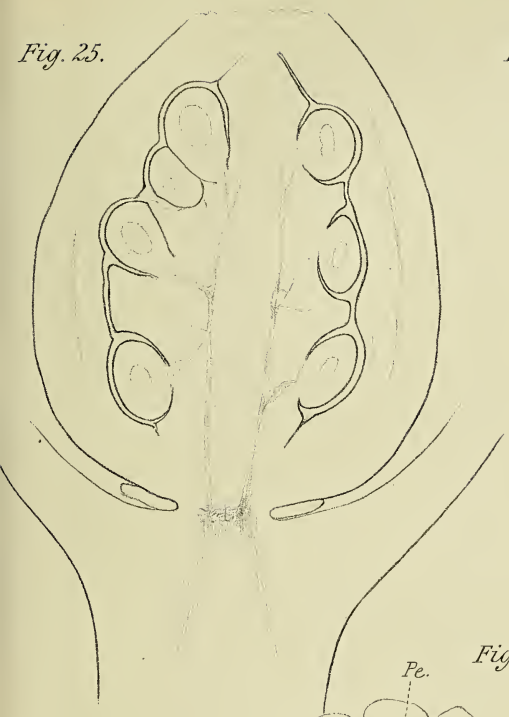

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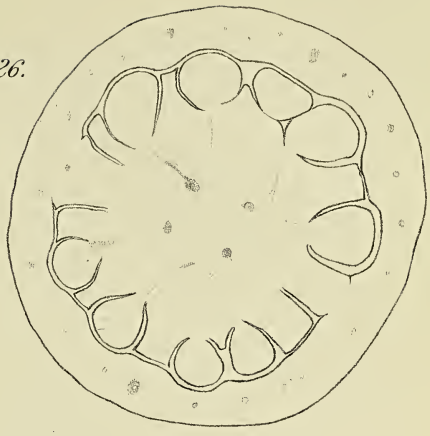

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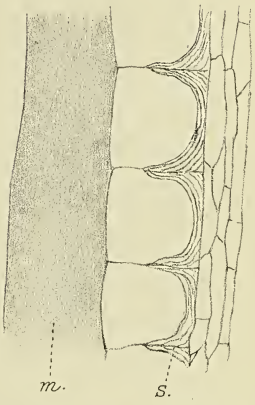

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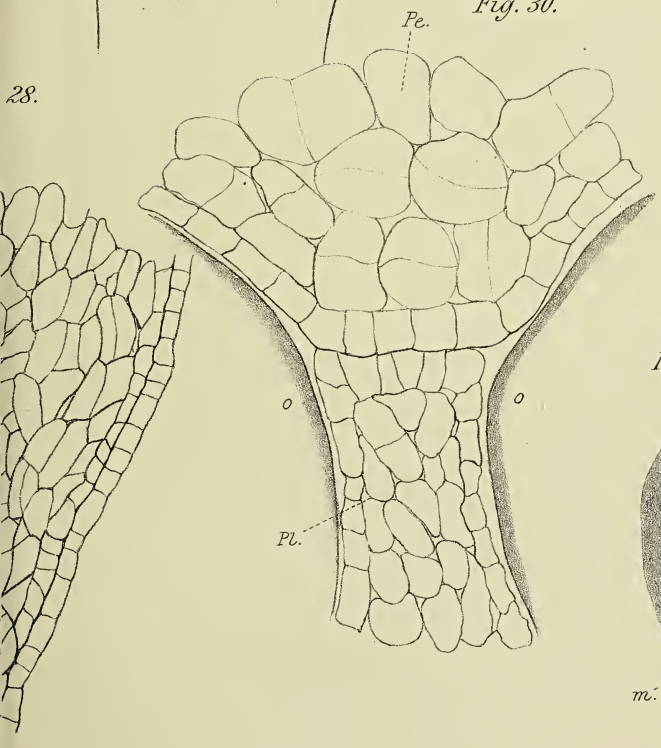

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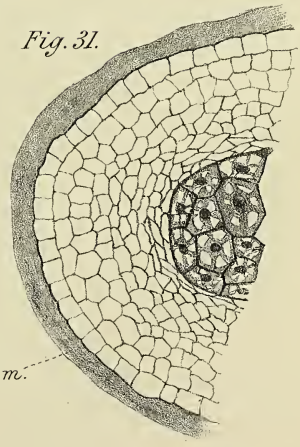

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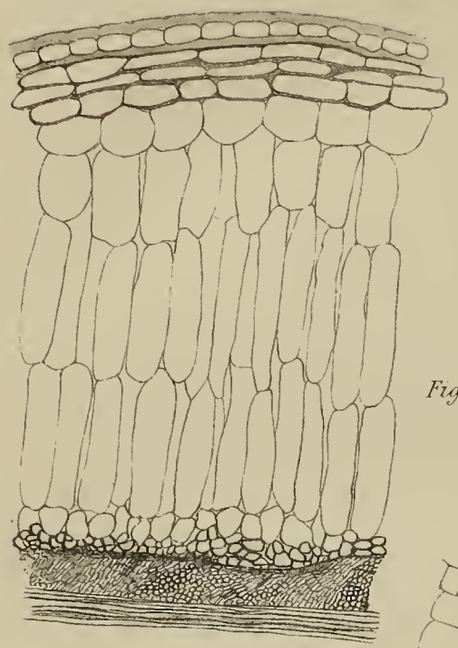

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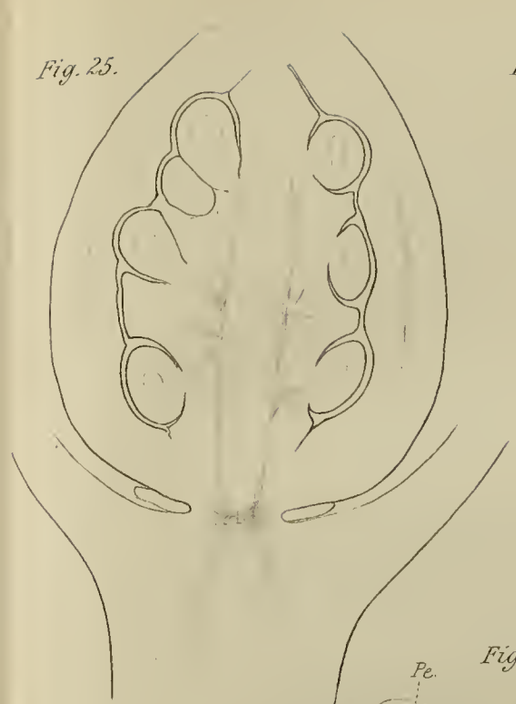

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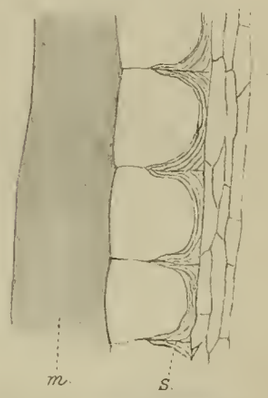

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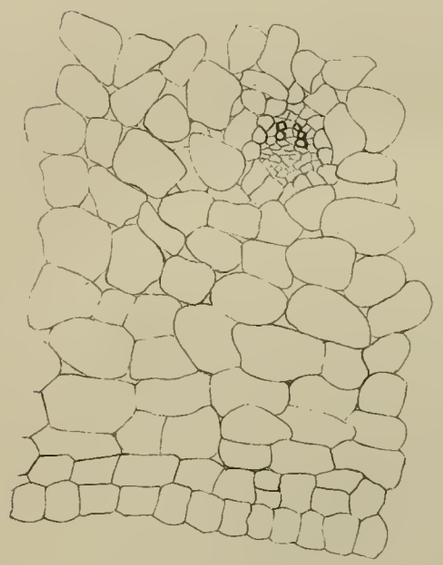

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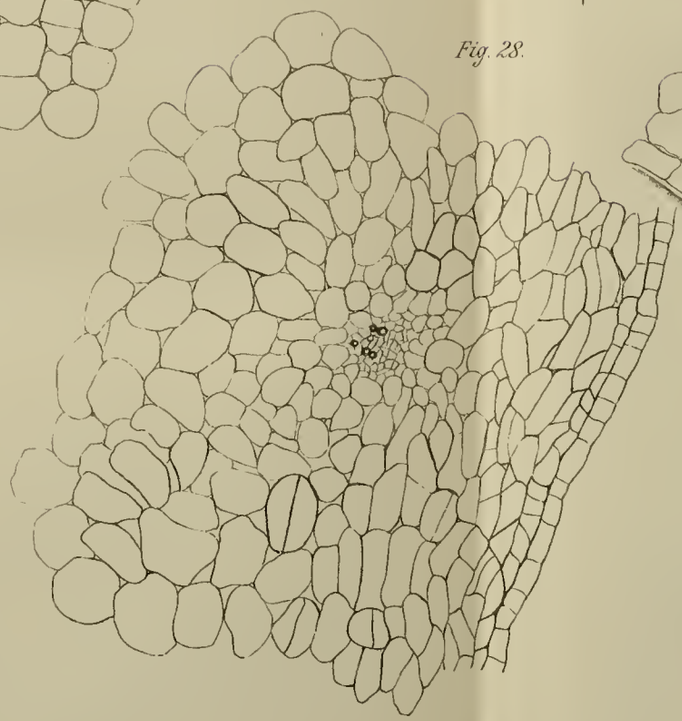

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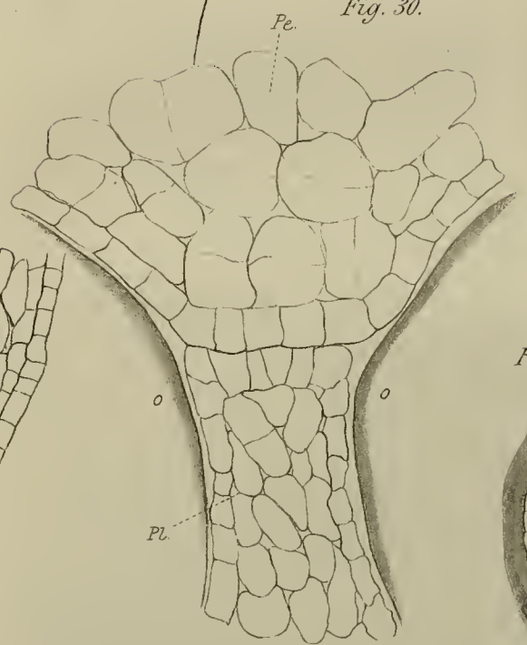

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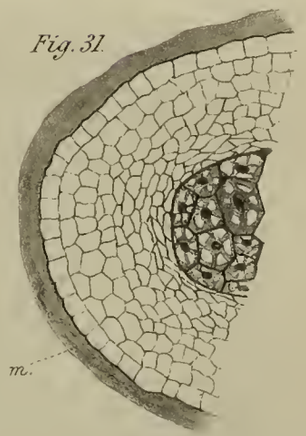

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On Epinasty and Hyponasty.

BY

SYDNEY H. VINES.

With Woodcuts 7 and 8.

THE analysis of the conditions which determine the position assumed by dorsiventral members in the course of their growth is a problem which, though it has engaged the attention of many observers, cannot as yet be regarded as completely solved.

In giving a brief historical outline of these observations, noting the gradual growth of knowledge on the subject, the first which need be considered are those of Frank[1]. As the result of a long series of experiments he came to the conclusion that dorsiventral members possess a peculiar form of irritability to the directive influence of light and of gravity, in virtue of which they place their flat surfaces perpendicularly to the direction of incidence of the rays of light or of the action of gravity, in such wise that the normally superior surface of the member is turned to the light, in the one case, and is uppermost in the other. To these phenomena Frank gave the names Transverse Heliotropism and Geotropism respectively,—names which are now commonly replaced by the less cumbrous terms Diaheliotropism and Diageotropism, suggested by Darwin.

[1] Frank: Die natürliche wagerechte Richtung von Pflanzentheilen, etc., Leipzig, 1870. For a full discussion of this subject see Vines, Lectures on the Physiology of Plants, Cambridge, 1886, Lectures 17 and 18. I purposely omit all reference to observations on the *torsions* of these members, as my own researches only refer to these incidentally.

[Annals of Botany, Vol. III. No. XI. August, 1889.]

It must be pointed out, however, that whilst it appears from Frank's observations that all dorsiventral members are diaheliotropic, it is not equally clear that they are all diageotropic; in fact, this appears to be rather the exception than the rule. Frank, for instance, states that, in most cases, members which are more or less horizontal under normal conditions and when exposed to light, grow erect in darkness in consequence, as he suggests, of negative geotropism. He cites, as examples of this, the creeping shoots of *Lysimachia nummularia*, *Polygonum aviculare*, *Atriplex latifolia*, and other plants, radical leaves, and the thallus of *Marchantia*.

The next paper to be noticed is that of De Vries[1], which consists largely of a criticism of Frank's theory of diaheliotropism and diageotropism. The main contribution which he makes towards a knowledge of the subject is the fact that the growth of the two opposed sides of dorsiventral members is unequal, and that this unequal growth is apparently due entirely to inherent conditions. When the growth of the upper surface is the more active, De Vries terms the member *epinastic*; when that of the lower, *hyponastic*. He observed that, as a rule, leaves are hyponastic at first, becoming epinastic in the latter part of their period of growth.

De Vries' contention, as against Frank, is that the assumption of peculiar forms of heliotropic and geotropic irritability in the case of dorsiventral members, is unnecessary and unwarranted by the facts. He endeavours to show that the various positions assumed by dorsiventral members can be accounted for as being due to various combinations of epinasty, hyponasty, negative or positive heliotropism or geotropism, the weight and balancing of the parts; discarding altogether the idea of diaheliotropism and diageotropism.

In his important paper on orthotropic and plagiotropic members, Sachs[2] touches upon this subject, and his views

[1] De Vries: Ueb. einige Ursachen der Richtung bilateralsymmetrischer Pflanzentheile, Arb. d. bot. Inst. in Würzburg, I, 1874.

[2] Sachs: Ueb. orthotrope und plagiotrope Pflanzentheile, Arb. d. bot. Inst. in Würzburg, II, 1879.

may be gathered from what he says with reference to the thallus of *Marchantia*. The plagiotropism of the thallus of *Marchantia* is, he says, to be ascribed to (negative) geotropism, to positive heliotropism (of the under side), and to the epinasty of the upper side. In the earlier part of his paper he speaks of the negative heliotropism of the thallus, but he explains that this apparent negative heliotropism is in fact the hyponasty of De Vries. Sachs' conclusions, therefore, go to confirm De Vries' dissent from Frank's theory of diaheliotropism.

Wiesner's[1] conclusions may next be briefly stated. He is of opinion that the ultimate position of dorsiventral leaves is the resultant of the opposing forces, negative heliotropism and negative geotropism: the leaf, which at first tends to rise by negative geotropism, is brought into the most favourable light-position by negative heliotropism, and is retained in that position because these conditions of illumination are those which most strongly resist negatively geotropic curvature.

The next paper on the subject, that by F. Darwin[2], is one which marks a distinct advance. By experiments with the clinostat he ascertained that dorsiventral leaves tend to place their normally upper surfaces at right angles to the incident rays of light. The importance of these observations is, that they go far to invalidate De Vries' argument against Frank, inasmuch as they show that the position in question is assumed by dorsiventral leaves under conditions in which gravity, whether as regards geotropic stimulation or the balancing of the parts, is inoperative. The conclusion 'that the power which leaves have of placing themselves at right angles to the incident light is due to a specialised sensitiveness to light—diaheliotropism—which is able to regulate or govern the action of other external forces, such as gravitation, or of internal

[1] Wiesner: Die heliotropischen Erscheinungen im Pflanzenreiche, Denkschr. d. Math.-Naturwiss. Klasse d. K. Akad. d. Wiss. Wien XXXIX, Part 2, p. 58, 1880.

[2] F. Darwin: On the power possessed by leaves of placing themselves at right angles to the direction of incident light. Journal Linnean Society, XVIII, London, 1881. See also 'Movements of Plants,' 1880.

forces, such as epinasty,' is strongly in favour of Frank's views. F. Darwin also confirms Frank's statement that radical leaves are negatively geotropic (apogeotropic), at least in the case of *Ranunculus Ficaria,* and notes also that radical leaves under normal conditions are epinastically pressed against the ground.

Another paper which must be noticed, but which can hardly be regarded as contributing much to the elucidation of the subject, is that of Detmer[1]. From observations on the effect of darkness and light on the expansion of leaves, Detmer came to the conclusion that epinasty is not, as De Vries thought, spontaneous, but is induced by the action of light; that it is what he terms 'a paratonic nutation-phenomenon.' He therefore suggests that the word 'photo-epinasty' should be substituted for 'epinasty.' It may be pointed out that he omits to refer at all to hyponasty; but of course if epinasty is not spontaneous, it is impossible to avoid the inference that the same is true of hyponasty, and the assumption of 'photo-hyponasty' is therefore inevitable, though Detmer does not carry out his views to this logical conclusion.

Vöchting[2] has made some interesting observations on the assumption of the fixed light-position by the leaves of certain Malvaceae, and comes to the somewhat ambiguous conclusion that the hypothesis upon which Frank bases his idea of transverse heliotropism is incorrect, though, as far as the facts go, Frank is on the whole right. With regard to the lamina, Vöchting considers that the effect of light is to bring it into that position in which it receives the maximum of incident rays. With regard to the petiole, it is stated to be negatively geotropic, positively heliotropic, and persistently epinastic in its basal portion.

Finally, there is an important paper by Krabbe[3] in which he arrives at the general conclusion that the light-position of leaves cannot be explained by ascribing it to simple combina-

[1] Detmer: Ueb. Photoepinastie der Blätter, Bot. Zeitg. 1882.

[2] Vöchting: Ueb. die Lichtstellung der Laubblätter. Bot. Zeitg., 1888.

[3] Krabbe: Zur Kenntniss der fixen Lichtlage der Laubblätter. Pringsheim's Jahrb. f. wiss. Bot. XX, Heft 2, 1889.

tions of directive forces, such as heliotropism, epinasty, etc., but is, on the contrary, the expression of a special heliotropic property. He shows that the weight of the leaves does not in any way affect their movements, and ascertains, by clinostat-experiments in darkness on *Phaseolus*, *Dahlia*, *Fuchsia*, and other plants, that when leaves are unaffected by any external directive influences, they exhibit well-marked longitudinal epinasty. It is not necessary to go into all the details of the paper, as they deal chiefly with torsions, a part of the subject into which I do not propose to enter at present. It need only be noted that he considers the leaves of *Dahlia* to be negatively geotropic.

Coming now to my own observations, I must premise that the general method of experiment was arranged, and many of the experiments made, before I was aware of the publication of Krabbe's paper. The object in view was to ascertain (1) whether epinasty and hyponasty are spontaneous movements, or are induced by light or other causes as stated by Detmer; and (2) whether the curvatures of dorsiventral members which, as pointed out in the foregoing historical sketch, have been hitherto ascribed to negative geotropism, are or are not due to this cause. I may at once give the conclusions to which I have been led: (1) Epinasty, and also hyponasty, are not induced, but are spontaneous movements; (2) dorsiventral members, so far as my experiments go, are not negatively geotropic, the movements hitherto ascribed to negative geotropism being due to hyponasty, and altogether independent of the action of gravitation.

The first series of experiments were extremely simple. Detmer based his theory of photo-epinasty on the observations that (1) the cotyledons of seedlings of *Cucurbita* remained closed up, with their upper surfaces in contact, when kept in continuous darkness for ten days, but they at once began to separate when, at this age, the plants were exposed for three to five hours to bright diffuse light; and (2) that the laminae of the primordial leaves of *Phaseolus*, kept in continuous darkness for fourteen days, presented a folded or

crumpled appearance, in consequence of hyponastic growth; but after an exposure for three to five hours to bright diffuse light the laminae began to flatten out and to become smooth. In both cases the exposure to light was followed by epinastic growth of the laminae. With the view of testing the accuracy of these statements with regard to the cotyledons of *Cucurbita*, I kept a large number of seedlings of both *C. ovifera* and *C. Pepo* in darkness for twenty days (June 10–30), and I found that in a large majority of cases the cotyledons separated more or less widely, the separation becoming first apparent about the sixth day. They were, however, exposed to feeble light for a few moments, not more frequently than once in twenty-four hours, for the purposes of observation, but this exposure can hardly be taken into account. Similar observations on the primordial leaves of *Phaseolus* proved the accuracy of Detmer's statement that the laminae do not become fully expanded in darkness.

These observations of mine suffice to prove that, in the case of *Cucurbita*, epinastic growth can take place in darkness, and thus, on the matter of fact, Detmer's theory is shown to be untenable. It is open to the further criticism that the phenomena which he describes are capable of another and a simpler explanation. Light certainly promotes the epinastic growth of the leaves in question, but there is no evidence that it initiates this growth; the effect of light is not '*paratonic*,' as Detmer would have it to be, but it is '*phototonic*.' The epinastic growth of the laminae, when exposed to light, is well marked, not because light induces photo-epinasty, but because the leaves are in the epinastic stage of their growth; so that when, under the influence of light, they regain the phototonic condition and resume their growth, that growth is necessarily epinastic.

The second series of experiments were made on plants other than those which Detmer observed, and had as their object the determination of the growth-movements of dorsiventral members when removed either from the directive influence of light alone; or, by means of the clinostat, from that of both

light and gravity. The general method of experimentation was the following. Plants were placed in darkness in the normal position, and the effect of these conditions upon the position of the leaves or other dorsiventral members was carefully noted at intervals of generally twenty-four hours. Other similar plants were rotated on the clinostat in darkness, and the effect observed as in the former case. By comparing the behaviour of the members in the two cases, it was possible to draw some conclusions as to the influence of gravitation upon the growth of the members under observation. All the plants were grown in pots; and, when on the clinostat, were so placed that the long axis of the plant coincided with that of the machine.

It will be convenient to arrange my observations according to the results which I obtained; that is, in accordance with the more striking epinastic or hyponastic growth.

1. Observations on Epinastic Members.

These observations were all made on dorsiventral foliage-leaves. The following is a typical case. A seedling of *Helianthus annuus*, about 40 cm. high, with four whorls of leaves (generally three leaves in each whorl in the plants used), in addition to the cotyledons and the apical bud, had been grown under normal conditions and fully exposed to light. Hence, at the beginning of the experiment, the leaves were approximately horizontal. The effect of being kept for twenty-four hours in darkness in the normal position was that the leaves of the upper whorls, especially the second and third, showed a strongly marked downward curvature. In the younger leaves this curvature extended throughout the whole length of the leaf from the apex to the insertion; in the older, but still growing leaves, the curvature was confined to the petiole. The oldest leaves, having ceased to grow showed no change in position.

The remarkable difference in the appearance of the plant,

before and after being kept in darkness is shown in the accompanying figures.

The curvature in question is not due to flaccidity of the tissues, for the leaves are fully turgid after their sojourn in darkness, and when an attempt is made to lift them up into the horizontal position they spring back into the recurved

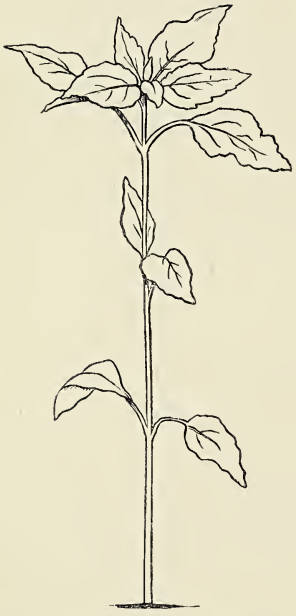

FIG. 7. Normal plant of *Helianthus annuus*.

FIG. 8. Same plant after twenty-four hours in darkness.

position with considerable force. Moreover, the leaves show the same curvature, and in the same time, when (*a*) the plant is rotated on the clinostat in darkness, and (*b*) when the plant is placed upside down in darkness.

On being again exposed to light, the recurved leaves regain the horizontal light-position within twenty-four hours.

Precisely similar results were obtained on repeating these

experiments with *Helianthus dentatus*, *H. tuberosus*, *H. pubescens*, *Dahlia variabilis*, *Fuchsia serratifolia*, and *Urtica urens*. The leaves of *Mirabilis Jalapa* behaved in a similar manner, but the curvature was slower and less marked than in the other cases. My observations as to the position assumed in darkness by the leaves of *Dahlia* and *Fuchsia* precisely agree with those of Krabbe, who used these plants in his experiments.

I made more prolonged observations (four days) on *Helianthus dentatus* on the clinostat in darkness. At their first development in the apical bud, the leaves, under these circumstances, are perfectly straight, so that their long axes are in a line with that of the stem; then they gradually curve outwards, throughout their whole length, until their long axes are at right angles to that of the stem, and finally curve backwards till their apices touch the internode behind their insertion.

In making these observations I was reminded that Batalin[1] had observed that the growing leaves of certain plants fall, whilst others rise, at night; and it occurred to me that possibly the former would react under experiment in the same manner as those which I had already observed. Batalin mentions *Impatiens parviflora*, *Polygonum Convolvulus*, and *Sida Napaea*, as plants whose young leaves fall at night. I made experiments with the two former, and found that they reacted in much the same way as *Helianthus*. The leaves of *P. Convolvulus* show this peculiarity when growing in darkness, whether on the clinostat or in the normal position, that, as they become longitudinally recurved, the lamina becomes revolute, curving inwards on both sides towards the under surface of the midrib.

There can be no doubt that these curvatures of the leaves are due to epinasty; either, as in most of the cases, to longitudinal epinasty alone, or, as in the case of *Polygonum Convolvulus*, to both longitudinal and transverse epinasty.

Nor can there be any doubt, in view of the conditions of

[1] Batalin: Ueb. die Ursachen der periodischen Bewegungen der Blumen- und Laubblätter. Flora, 1873.

the experiments, that the epinasty was spontaneous. These observations, taken in conjunction with those on the seedlings of *Cucurbita*, seem to prove conclusively the falsity of Detmer's theory of photo-epinasty.

If any further evidence is required, it is afforded by my observations on *Primula officinalis*, which has proved itself to be most instructive. If a plant be taken which has been growing fully exposed to light, it will be seen that the older radical leaves are more or less nearly horizontal; those next in age, obliquely ascending; and the youngest very nearly, but not quite, vertical. On being placed in darkness in the normal position, the first change to be noticed is that the younger leaves become quite vertical, whilst the older leaves, though still growing, remain horizontal. About the fourth day in darkness it will be observed that the lamina of the youngest leaves is being developed in a revolute manner, whilst, at the same time, they curve outwards throughout their whole length: at the same time the older, but still growing leaves, instead of being horizontal, have become arched, their apices being firmly pressed against the soil. About this time (sixth day) growth ceases, and the positions remain unchanged.

Exactly the same phenomena are exhibited when the plant, instead of being placed in the normal position, is rotated on the clinostat.

The natural interpretation is, that the movement of the youngest leaves into line with the long axis of the plant when first placed in darkness is due to hyponasty, whilst the subsequent curvature outwards, away from this line, is due to epinasty. In other words, the leaves of *Primula* are hyponastic at their first development, becoming subsequently epinastic, at the time when the expansion of the lamina begins, and remaining so until growth ceases.

Somewhat similar results to those recorded of *Primula* were obtained with *Vicia Faba*. At their first development the long axis of the leaf is nearly parallel to that of the stem, the lamina of each leaflet being longitudinally infolded; in other

words, the leaf is hyponastic. This position is retained in darkness, both when the plant is in the normal position and when it is rotated on the clinostat. Under normal conditions, the leaves, as they develope, become epinastic; the petiole sinks, and the laminae of the leaflets flatten out. Leaves in this stage of development show epinastic curvature in darkness, both in the normal position and on the clinostat; but I have never succeeded in observing, in darkness, that transition from the hyponastic to the epinastic growth which is so marked in *Primula*, as the leaves of *Vicia* are apparently incapable of growth for more than a very short period under these circumstances.

2. Observations on Hyponastic Members.

In describing the foregoing observations on *Primula* and *Vicia*, I have assumed, without explanation, that the rising up of the youngest leaves of the former in darkness, and the position taken up by the leaves of the latter at their first development, are due to hyponasty. The only other possible supposition is that gravitation is the active cause. But, inasmuch as these phenomena are equally apparent when the plants are rotated on the clinostat in darkness, it is clear that they cannot be due to gravitation. They are, in fact, spontaneous, and can only be ascribed to the more rapid growth of the lower side of the leaf, that is, to hyponasty.

Still more convincing evidence of the spontaneous nature of hyponasty is, however, forthcoming. As the assumption that dorsiventral leaves are negatively geotropic seems to rest chiefly upon observations made upon radical leaves, I did not content myself with observing only *Primula*, but extended my observations to two other plants, *Plantago media* and *Taraxacum Dens-Leonis*, with the following results.

Plantago media. A plant which had been growing fully exposed to light, the leaves of which were, consequently, expanded horizontally, was kept in darkness in the normal position for seventy-two hours. The young leaves gradually

rose up from the horizontal position, the youngest ones becoming erect. At the same time the rising leaves became strongly involute, the lateral margins of the lamina being curved inwards towards the upper surface of the midrib. The older leaves showed marked epinasty.

A similar plant was, at the same time, rotated on the clinostat in darkness for seventy-two hours. The leaves of this plant behaved in precisely the same manner as those of the plant in the normal position.

The leaves of a plant which have risen in consequence of having been kept in darkness, return to the horizontal position in two or three days when exposed to light.

Taraxacum Dens-Leonis. The leaves of this plant behave in a quite similar manner to those of *Plantago*, except that the transverse hyponasty is less marked.

The change of position of the young radical leaves of these plants in the normal position in darkness was described by Frank, and was attributed by him to negative geotropism,—an explanation which seems to have been hitherto accepted without question. The clinostat-experiments, however, prove that this explanation is not in accordance with fact. The movements can only be due to hyponasty, both longitudinal and transverse. These leaves present the peculiarity that the change from the hyponastic to the epinastic phase of growth takes place at a relatively late stage in their development.

Remembering Batalin's observation, to which reference was made above, that certain growing leaves rise at night, such as those of *Chenopodium*, Cabbage, *Polygonum aviculare*, *Stellaria*, *Linum*, etc., I made some observations on two of the plants mentioned by him, namely *P. aviculare* and *Linum usitatissimum*. I found that, when placed in darkness for twenty-four hours, in the normal position, the previously horizontal younger leaves of these plants rose up hyponastically, becoming erect, and that the same effect followed in darkness when the plant was rotated on the clinostat.

A more important observation was made with *Marchantia*. A plant growing in a pot was placed in the normal position

in the dark chamber exposed to weak diffuse light entering through a side-window, a mirror being placed behind the plant so as to equalise the illumination on the two sides. Another plant was rotated on the clinostat under the same conditions of illumination. The position of the plant on the clinostat was such that the flat surface of the thallus was at right angles to the long axis of the machine, and that the direction of the incident rays of light was perpendicular to the long axis of the machine, and parallel to the flat surface of the thallus. The same window and mirror illuminated both plants. Exposure to light was considered necessary in view of the probably long duration of the experiment; but it is evident that, under the conditions of the experiment, no heliotropic effect could be induced.

The experiment commenced on July 29, and continued until August 9. In three days the ends of many of the branches of the thallus commenced to curve away from the surface of the soil in both the plant in the normal position and that on the clinostat, and this position was retained and became more marked throughout the duration of the experiment.

It is on this observation and those which precede it that I base the conclusion that the curvatures of dorsiventral members which have hitherto been ascribed to negative geotropism are not due to this cause, but are the expression of an inherent more active growth of the lower side, that is, of hyponasty.

The results which I have obtained establish conclusively that epinasty and hyponasty are important factors in determining the position assumed by growing dorsiventral members; and that therefore no observations on the action of gravity or of light on such members are conclusive unless the hyponastic or epinastic state of the member has been previously ascertained and duly taken into account.

With this I conclude the account of my principal observations, and it only remains to briefly discuss the various forces which determine, in the plants which I have observed, the position assumed by the dorsiventral members under normal

conditions, and to mention one or two experiments on geotropism which I have made by the way.

Taking first the case of the epinastic members, it may be assumed that there are three forces at work; their own epinasty, the action of light, and the action of gravitation. The tendency of epinasty, in the case of leaves, is to bring the lamina into the vertical plane, the apex being directed downwards.

When an epinastically recurved leaf is exposed to vertical light of sufficient intensity, the effect is to raise the lamina into the horizontal plane so that its upper surface is at right angles to the direction of the incident rays. From this I conclude that the lamina is diaheliotropic. Doubtless the influence of gravitation promotes the assumption of the horizontal position; but it is clear that this is mainly due to the action of light, since gravitation is incapable of preventing epinastic curvature in darkness when the plant is in the normal position.

With regard to the influence of gravitation in determining the position of epinastic dorsiventral members, I inferred from my observations which prove that hyponastic members are not negatively heliotropic, that this is true also of epinastic members; in fact, that no dorsiventral member is negatively geotropic. Though I do not claim to have fully investigated the matter, I have made some observations on epinastic members which tend to prove, not only that they are not negatively geotropic, but that they are diageotropic. The following case will explain the mode of experimentation. A young plant of *Helianthus annuus*, growing in a pot, its stem being firmly secured to a stick to prevent geotropic curvature, was placed in darkness with its long axis horizontal. In this position of the stem, the two youngest leaves were situated, the one on the upper surface, the other on the lower surface of the horizontal stem, the apex of the former pointing vertically upwards, that of the latter vertically downwards. The phyllotaxis of *Helianthus* being opposite and decussate, the two leaves of the next whorl were situated one on each side of the horizontal

stem, their surfaces being now vertical. By the fourth day of the experiment the following changes in position had been effected. Of the youngest pair of leaves, the upper had recurved so that its upper surface had come to be nearly horizontal; the lower had only slightly changed its position, having risen somewhat out of the vertical plane in the acropetal direction. The two leaves of the second whorl both exhibited marked epinastic curvature, and their petioles had undergone torsion through nearly a right angle, so that, in both, the upper surface of the lamina was directed upwards, though it was not flat on account of the epinastic curvature. Similar results were obtained with *H. pubescens* and with *Dahlia variabilis*.

It must be borne in mind, in the interpretation of these facts, that the leaves were strongly epinastic, and there can be no doubt that the changes in position were due partly to this cause and partly to the action of gravitation. If, now, an explanation be attempted on the assumption that the leaves are negatively geotropic, it will be found to be impossible. Taking first the youngest pair of leaves, the upper leaf, being vertical, is in the position of stable equilibrium as regards negative geotropism; hence its curvature into the horizontal plane must be due to epinasty acting powerfully in opposition to negative geotropism. With regard to the lower leaf, inasmuch as it could hardly have been absolutely vertical, it is probable, on the theory of its negative geotropism, that gravitation tended to raise it into precisely the opposite position to that in which it was originally placed, and this effect was to some extent realized in the observed change of position. In this case, then, negative geotropism succeeded in overcoming epinasty. But this conclusion is in direct contradiction to that arrived at with regard to the upper leaf. Inasmuch as the two leaves belonged to the same whorl, they must have been in the same epinastic stage of growth; hence, it is impossible to assume that in the one case epinasty overcame negative geotropism, whilst in the other negative geotropism overcame epinasty.

The explanation which I would offer as a substitute is based on the assumption that the leaves are diageotropic; that is to say, that their reaction to the action of gravitation is to place themselves in the horizontal plane with their morphologically upper surfaces facing the zenith. From this point of view, the change in position of the upper youngest leaf is ascribed to epinasty acting together with diageotropism; and the change in position of the lower youngest leaf to diageotropism acting in opposition to epinasty. It may be objected with reference to this last statement, that it is inconsistent with the fact which I have brought prominently forward, that the young leaves of *Helianthus* show marked epinastic recurvature in darkness, which can only be explained on the assumption that here epinasty has overcome diageotropism. This objection is, however, without weight. The two statements are found to be perfectly consistent when it is remembered that the effect of gravitation depends upon the angle at which it acts. Now, in the case of a plant in the normal position, the effect of diageotropism on the horizontal leaf is at its minimum, increasing as the leaf-surface forms a larger angle with the horizontal, and attaining its maximum when the leaf points vertically downwards. Hence a leaf, under such conditions, sinks below the horizontal because epinasty is more powerful than diageotropism in that position, and continues to do so until a position of equilibrium is reached. In the special case now under consideration, the leaf, pointing vertically downwards, is in that position in which diageotropism exerts its greatest influence, an influence, as it appears, sufficiently strong to prevent epinastic curvature and even to raise the lamina somewhat towards the horizontal position. The phenomena presented by the two youngest leaves can, therefore, be explained more satisfactorily on the theory of diageotropism than on that of negative geotropism. The phenomena presented by the leaves of the second whorl, cannot be at all explained on the theory of negative geotropism, but only on that of diageotropism; this is sufficiently obvious to render any detailed discussion unnecessary.

I may note, in passing, that Krabbe assumes that the leaf of *Dahlia* is negatively geotropic, and he does so for the following reason. He observed that the leaf does not exhibit epinastic curvature when in the normal position and exposed to light, whereas it does exhibit this curvature when exposed to light on the clinostat. From this he concludes that the heliotropic effect of light is insufficient, by itself, to counteract epinasty; and that the horizontal position of the leaf under normal conditions is due to the combined influence of light and of gravitation in opposition to epinasty, the latter, as he suggests, producing a negatively geotropic effect. The facts do not, however, justify this conclusion. They may be accounted for on the assumption that the light to which Krabbe exposed the plant in his clinostat-experiments was not sufficiently intense to induce the full heliotropic effect. But apart from this assumption, his observations only prove that gravitation has some effect, though the facts give no indication of the nature of the effect. In accordance with what I have stated above, I believe the effect of gravitation in *Dahlia* to be diageotropic, and I would point out that Krabbe's observation can be explained quite satisfactorily from this point of view.

With regard to hyponastic members, it may be assumed that here also there are three forces which determine their position: their own hyponasty; the action of light; the action of gravitation. The tendency of hyponasty is to raise the member so that its long axis approaches the vertical. The effect of light is, as in epinastic members also, to bring and retain the member in the horizontal position—that is, it is, I believe, diaheliotropic. The effect of gravitation is, as I have clearly proved, certainly not to produce negatively geotropic curvature, but is probably diageotropic.

I have made some experiments on hyponastic members, similar to those on epinastic members described above, with the object of ascertaining whether or not they are diageotropic. A normal plant of *Plantago media*, growing in a pot, was placed in darkness with its long axis horizontal. Of the

numerous leaves, the seven youngest showed themselves to be hyponastic by rising away from the surface of the soil; the remaining leaves simply showed well-marked epinastic curvature and nothing more. The seven youngest leaves not only rose hyponastically, but they gradually assumed different positions according to their relation to the centre or axis of the plant. On the second day of the experiment—that is, after forty-eight hours in the horizontal position in darkness—their relative positions were as follows, the numbers used indicating the relative age of the leaves, No. 1. being the youngest. Leaf 1, inserted vertically below the axis, showed strong hyponastic curvature so that it curved completely over the growing-point; leaf 6, inserted almost directly beneath leaf 1, had curved upwards so that its upper surface was nearly horizontal; leaves 2, 5, and 7, were inserted above the axis, leaf 2 nearly vertically above it, leaf 5 obliquely on the left side, leaf 7 obliquely on the right side; these three leaves were slightly raised from the soil, but showed no other change of position; leaves 3 and 4 were inserted laterally on the axis, almost opposite each other, and showed, in addition to hyponastic curvature, torsion through nearly 90°, so that a part of their upper surfaces faced the zenith. On continuing the observation twenty-four hours longer, the only change observable was that leaf 6 had risen slightly above the horizontal, and that the youngest leaves began to be involute in consequence of transverse hyponasty. As I have already proved that the young leaves of *Plantago* are not negatively geotropic, it is useless to attempt an explanation of these phenomena based on the assumption of negative geotropism: it is only necessary to ascertain whether or not they are explicable on the assumption of diageotropism. Taking first the leaves inserted below the axis, the position of leaf 1 can be satisfactorily accounted for by supposing that, at this early age, hyponasty is so powerful that it altogether neutralises diageotropism: in accordance with this, the position of leaf 6 is due to diminished force of hyponasty, a consequence of its being older than leaf 1, which can only so far counteract diageotropism as to

raise the lamina slightly above the horizontal. Coming next to the leaves inserted above the axis, leaves 2, 5, and 7, the explanation becomes more difficult. In the case of leaf 2, hyponasty must be strong, and yet the only effect is the raising of the leaf slightly from the surface of the soil, when it might have been expected to cause the leaf to curve over downwards in the same way as it caused leaf 1 to curve over upwards. I believe the cause of the different hyponastic effect in these two leaves, of nearly the same age, is their relative position. The tendency of the hyponastic growth of leaf 2 was to bring the morphologically superior surface of the leaf into such a position that it would face downwards. Now this tendency is in direct opposition to the most striking effect of diageotropism, which is to bring the morphologically upper surface of the leaf in such a position that it faces the zenith. Hence the hyponasty of leaf 2, strong as it undoubtedly must have been, was insufficient to counteract diageotropism to any considerable extent in this position; and, as torsion seems to have been physically impossible, no change of position took place. If this explanation is adequate in the case of leaf 2, it must apply also to leaves 5 and 7, in which, as they were older, hyponasty was less powerful. In the two lateral leaves, Nos. 3 and 4, both hyponasty and diageotropism produced their full effects, the one in curvature, the other in torsion. Similar results were obtained with *Taraxacum Dens-Leonis*.

It may be urged, in criticism of these views, that I have assumed diaheliotropism without adducing any evidence in support of the assumption. In reply I would submit that my observations do afford definite evidence on this important point. It appears to me to be quite impossible to explain the return to the horizontal, when exposed to sufficiently intense light, of members which have become curved either epinastically or hyponastically in consequence of having been kept in darkness, in any other way than by attributing it to the influence of the light on their diaheliotropic irritability. It is true that gravitation co-operates in inducing this return to the horizontal, but the fact that hyponastic or epinastic curvature

takes place in darkness when the plant is in the normal position proves that gravitation alone cannot determine the assumption and maintenance of the horizontal position.

My observations lead me to the conclusion that the forces which are active during growth under normal conditions in determining the position of dorsiventral members, are their own inherent hyponasty or epinasty; the action of light producing a diaheliotropic effect; the action of gravitation producing a diageotropic effect. The ultimate position assumed is, I believe, a fixed light-position, the influence of light being the most powerful factor. Light can, as F. Darwin's experiments prove, overcome epinasty or hyponasty; and these can overcome the influence of gravitation, as I have shown, except when in so doing they would bring the morphologically upper surface of the member to face downwards, a possibility which is not often realised in plants growing in the normal position.

The conclusions at which I have arrived with regard to growing members appear to me to be equally applicable to motile foliage-leaves. So far as I am aware no explanation has as yet been offered of the differences in the nyctitropic movements of leaves; of why it is that some motile leaves rise, and others fall at night. These differences may be explained on the assumption that motile leaves, like growing leaves, may be either epinastic or hyponastic; that is to say, they may be in a state of epinastic or hyponastic tension, though the tension is not associated with actual growth. Motile leaves which fall at night do so, apparently, because their epinastic tension is no longer counteracted by diaheliotropism; similarly, leaves which rise at night do so because their hyponastic tension is no longer counteracted by diaheliotropism. The former behave like, for instance, the growing leaves of *Helianthus* when placed in darkness; the latter, like the younger leaves of *Plantago*. This view is simply a natural consequence of the remarkable similarity between the nyctitropic movements of growing leaves, as described by Batalin, and those of motile leaves; it can hardly be doubted

that an explanation which holds good in the one case is correct in the other.

So far I have dealt exclusively with dorsiventral members which, when fully exposed to light of sufficient intensity, place their upper surface at right angles to the incident rays; to members, that is, which are diaheliotropic. But it must not be overlooked that there are dorsiventral members which take up a different light-position, presenting their margin to the incident rays, and which have hence been described as paraheliotropic. This phenomenon is presented both by young growing leaves and by mature motile leaves. So far as I am aware, no observations have been made on growing leaves of this kind with the view of ascertaining whether they are epinastic or hyponastic, and I have not had time this season to make any experiments with them. But some inferences can be drawn as to the conditions of paraheliotropism in mature motile leaves, at least in those cases, which seem to be relatively few, in which the paraheliotropic movement is not effected by means of torsion. For example, Darwin[1] has pointed out that the leaflets of *Robinia* fall at night, whereas when exposed to bright sunlight they rise above the horizontal. In accordance with what has been said above in explanation of nyctitropic movements, that of the leaflets of *Robinia* may be ascribed to epinasty. The assumption of the paraheliotropic position is, therefore, effected in opposition to the inherent epinasty of the leaflets.

In *Averrhoa bilimbi* the leaflets fall downwards at night until they are vertical, and are therefore probably epinastic like those of *Robinia*. But they likewise sink on exposure to bright light into an obliquely descending position, so that the effect of the inherent epinasty of the leaflets is modified to only a slight extent.

This kind of reaction to light cannot, I think, be satisfactorily explained otherwise than on the assumption of a special paraheliotropic irritability.

There remains to be considered yet another class of move-

[1] Darwin: Movements of Plants, p. 445.

ments which are affected by light, those, namely, of highly sensitive members such as the leaves of the Sensitive Plant (*Mimosa pudica*) and the perianth-leaves of many flowers. It is well known that the leaflets of *Mimosa* close on being placed in darkness, and open on being again exposed to light, and that many flowers close in darkness, or on diminution of the intensity of the light, re-opening when again exposed to light or when the intensity of the light is increased, whereas others close in light and open in darkness. In the attempt to analyse these phenomena, it must be first pointed out that the effect of light is quite different in this case from that in the cases previously discussed. In those cases it was directive or heliotropic; in these it is dependent, not upon the direction, but upon the intensity of the incident light. This is made clear by the fact that exactly the same movements can be induced by other means; in the leaflets of *Mimosa*, by a touch, in the perianth-leaves of flowers by variations of temperature. In the next place, it may be inferred from the observations described above, that the position assumed in darkness by a dorsiventral member is that which results from the conditions of tension inherent in the member. Hence the leaflets of *Mimosa*, and the perianth-leaves of flowers which close in darkness, are hyponastic; whereas the perianth-leaves of flowers which open in darkness are epinastic. The opening of the former, when exposed to sufficiently intense light, is due to the induction of epinastic tension; the closing of the latter, under the same circumstances, is due to the induction of hyponastic tension.

The movements of these leaves under the influence of light afford instances of true photo-epinasty and photo-hyponasty, as distinguished from those cases (*Cucurbita*, *Phaseolus*) to which Detmer applied this explanation; the essential difference being that, in these cases, light induces a tension which is precisely the opposite of that inherent in the leaf, whereas in Detmer's cases light merely rendered possible, by inducing phototonus, the external manifestation by growth of the conditions of tension inherent in the leaf.

I am conscious that the number of plants which I have observed is small; but, as they represent diverse groups, and as the forms of the members are various, the results obtained may be considered to be of wide application. I hope, however, to resume and extend my observations next spring.

NOTES.

ON TWO CASES OF LAMINAR ENATIONS FROM THE SURFACES OF LEAVES. 1. I have in the front-yard of my house a fine specimen of *Anthurium crassinervium*, Schott, which stands exposed to the full heat of our tropical sun. It has actually twelve leaves (70 to 75 by 20 to 25 centim.) and has flowered and fruited several times. The leaves stand nearly vertical, making angles of from 75° to 80° with the horizon, which gives the plant a strikingly compact appearance, whilst other specimens growing in the shade have a more or less expanded foliage, and do not look so crowded. This, of course, is due to the difference of insolation, the leaves of the first plant placing themselves to nearly vertical in order to avoid the fatal influence of excessive light. The effect is especially noticeable in the outer leaves, which bend abruptly in angles from 30° to 40° at the petiolary knob.

On the dorsal surface of two of the leaves there is quite a number of curious enations midway between the primary nerves, which form boat-like structures, about 2 centim. long, pointed at both ends, and measuring 5 to 8 millim. across the middle, whilst the laminar borders protrude 4 to 5 millim. from the surface of the blade. The inner side of these laminae presents the same appearance as the upper surface of the leaf, and their outer side is in every respect equal to its under surface. On the corresponding places of the upper surface of the leaf there is a linear impression, wholly covered by the epidermis. Two of the enations have remained in a very rudimentary state, and consist only of the upper impression just mentioned and a somewhat salient line on the under surface, which looks like the scar of a cut partially healed.

I had never before seen anything like it, although *Anthurium crassinervium* is a very common plant in our neighbourhood; nor do I remember having met with any published record of a similar observation made by others.

There is no difficulty in explaining the whole anomaly. It is a well-known fact that in several species of Aroideae the leaf-blade presents a certain number of oval or oval-oblong holes, which are the consequence of unequal growth, during prefoliation, in the tissues close to the primary nerves and those between them. Such holes, however, do not occur in *Anthurium crassinervium*; but in the case here described there must have been at least a first step towards their formation, that is to say, a slight break or rupture in the internerval tissue, just sufficient to neutralize the small amount of lateral traction. The leaf having an involute ptyxis, its under surface has of course a higher degree of tension than the upper one, and thus the two severed borders of the break would bulge out a little, but not enough to destroy the inner contact of the adjoining epidermis. The surface of the leaf at this period is moreover of a certain viscosity, which no doubt contributed to maintain adhesion and facilitated fresh coalescence on the ventral surface, whilst the free borders on both sides of the rupture-line continued to grow outwards and by little and little became the laminar enations mentioned before.

2. Some years ago a friend of mine gave me a leaf of the mango-tree (*Mangifera indica*, L.), which had on its under surface a secondary leaf growing from the midrib, and recently another mango-leaf was shown to me, where the accessory leaf belonged to the upper surface. Both secondary leaves are in the shape of little boats, adhering with their keel to the midrib of the primary leaf. Their own median nerve is evidently a piece of the outermost fibro-vascular bundles of the original costa, so that there is no free extremity. Like in similar instances recorded in works on teratology, the convex side of the accessory leaf is of the same appearance and structure as the adjoining surface of the large leaf.

Dr. Maxwell T. Masters mentions the case of an orange-leaf which appears to belong to the type here described; he abstains, however, from giving an explanation and says only what it cannot be [1].

I beg leave to proffer the following interpretation, which I believe is quite new, although based on facts well known to all those who have given some attention to the teachings of modern vegetable physiology.

[1] Veget. Teratology, 1869, p. 446. I have not seen the German translation of the work, which is said to contain many corrections and additions by the author; I therefore do not know whether the passage quoted above has been altered or not.

The midrib of the leaf is undoubtedly an organ which partakes of the properties of dorsiventral shoots, and the same character consequently must be inherent to all the fibro-vascular bundles of which it is composed, although it remains generally in a latent condition. It may, however, for one cause or another, acquire a greater potency and lead to a kind of individuation of any one bundle; which accordingly will behave as an independent dorsiventral shoot. This, I think, is especially possible in the outermost bundles, which form, on either side, the prominent edges of the midrib, on account of their more or less isolated and, to a certain degree, independent situation. Now in the mango-leaves mentioned, this is precisely what has happened, and so their accessory leaves were formed.

In both cases it is but natural that the epidermis and adjoining layers of the leaf-tissues should grow on either side without any alteration of structure over the nearest part of the lateral branches (or nerves) sprouting forth from the individualized bundle, and therefore the inner surfaces must be the same on either side of the primary leaf.

But then it follows from the polarity of the molecular nature of cells and tissues, that the opposite or exterior faces of each accessory leaf must be the reverse of the corresponding surfaces of the original leaf.

This explains the somewhat startling fact that a morphologically under surface is directed upwards towards the light, and *vice versa*, and gives additional support to the opinion that the difference of structure in the two surfaces of the lamina does not depend so much on external causes, as on the molecular conditions of the tissues and their cellular elements.

The concave shape of the accessory leaves is the result of unequal growth, the lower leaf being hyponastic, the upper one epinastic; because it is evident that the conditions of growth will be more favourable for the surface which is the direct continuation of the homologous surface of the primary leaf, and this so much the more as the geotropism of the dorsal side, and the heliotropism of the ventral one, in each case work in the same direction.

In conclusion, I think we have here a case of fission, but as to its primary cause, or causes, I am unable to proffer any suggestion. In the first of the two leaves described, there is on the midrib a very small knob just where the accessory leaf begins, and it is not

impossible that this knob has something to do with the whole structure.

The second leaf I had only for a few minutes in my hands, and unfortunately I forgot to make sure of this point before I returned the leaf.

A. ERNST,
University of Caracas, Venezuela.

NOTE ON THE PROPAGATION OF FERNS.—In raising ferns from spores it is possible to obtain almost any form that is aimed at, if spores can be obtained from the varieties to be changed in any wished-for direction. For example, if spores from a plumose form of *Athyrium*, *Polypodium*, or *Polystichum* be sown with any polydactylous forms of these species it is possible (and it has been accomplished) to raise plumose forms that are polydactylous; and we have now most beautiful polydactylous-plumose forms of *Athyrium*, *Polypodium*, and *Polystichum*. The plumose form is merely taken haphazard as an example, for the same may be said of forms that are cruciate, capitate, ramose, truncate, setose, sagittate, depauperate, multilobate, or linear, etc., or of the combinations of these forms.

One striking feature with regard to ferns is a similarity in the varieties of the various species.

The increase in the number of beautiful varieties has been very great during the past few years, and so much success has attended attempts to produce variation in form, that it seemed desirable to endeavour to obtain varieties that are variegated. This I have accomplished by sowing spores of *Scolopendrium crispum* and various other varieties together, and adding to these, spores of a variegated form; there have resulted young plants that are variegated, and which at the same time have the forms of all those sown together [1].

As might be expected, the more extraordinary the variety that is

[1] At the British Association Meeting at Bath a paper on Hybrid Ferns, by E. J. Lowe and Colonel Jones, was read, a note of which (with illustrations) appeared in the ANNALS OF BOTANY.

raised, the less likely is it that two will be alike, yet this occasionally happens, notably in the case of a very curious and distinct variety of *Athyrium*; and such singular examples convinced me that the duplication is to be accounted for by origin from one and the same prothallus. To test this a number of prothalli resulting from the sowing of a mixture of varieties of *Athyrium*, and also a similar number of *Scolopendrium* were transplanted singly a quarter of an inch apart, so that it was possible to divide a prothallus into several divisions at the time when the first fronds were springing up. It is not easy to detect the prothallus at the right moment; because, as the frond appears the prothallus dies away; yet the decay of the prothallus is not always as rapid as the growth of the frond, especially where the prothallus has a vigorous growth.

A number of these prothalli of both *Athyrium* and *Scolopendrium* were divided; in the case of the latter I succeeded in dividing in twelve instances a prothallus into two plants, and in four instances into three. In several instances where there was great vigour of growth, two prothalli had grown together and formed a complete interwoven mass that could not be separated, and had become to all intents and purposes one prothallus from which sprang up fronds having the same characters. In the case of these intergrown prothalli in two instances they have been divided into four plants, in two into five, in one into seven, and in one instance as many as ten plants (unmistakably alike) were divided from the double prothallus. Though yet small they cannot fail when mature to resemble each other in a greater or less degree.

If a number of prothalli are grown thickly together there is less vigour, they do not seem to blend or grow to any great size before the fronds appear, and in these circumstances no two of the resultant ferns are alike; it is, however, apparent that they have been generally impregnated, i. e. from all the varieties, because the young ferns consist of a series of plants that show a gradation of the forms of the varieties sown together, i. e. a series of plants having characters intermediate between the varieties experimented upon.

It is certain, then, that more than one plant can be produced from one prothallus, and these have a striking likeness to each other; and further, if two prothalli are allowed to grow together, they will affect each other, and produce plants having a strong resemblance to each other. We are speaking of the plants in their infant state, as none

have as yet arrived at maturity. The resultant fern may depend, not only upon the variety from which a spermatozoid sprang, and upon that which bears the mature archegonium in which the spermatozoid is deposited, but a further change may be produced by the coalescence of two prothalli.

It is the general notion that only one archegonium out of a number on each prothallus is impregnated. It appears to me that several archegonia (if in a mature state at the same time) may be impregnated, and twin or triplet plants be produced.

Transplanting the prothallus in the early stage before fronds are formed is a difficult operation, and the difficulty is increased if the endeavour is made to plant them singly; if very thickly sown this is almost impossible. I always advocate planting at an early stage, and the modus operandi is as follows:—Small indents are made on the smooth surface of the soil after first watering it with a fine rose. The point of a penknife lifts the prothalli, and a gentle pressure with the finger pushes it into the indent. The moist soil damps the finger so that it is requisite to dry it between each operation in order that the fern shall not adhere to it. Looking back some years to the time when the *Athyrium Filix-femina*, var. *Victoriae* was first discovered, I then used to raise spores in a modified Wardian case. This was kept under a shelf in a subdued light, and as the prothalli became mature, they were transplanted and placed in the full light of a greenhouse facing the north, and in this situation the fronds quickly appeared; not so those in the Wardian case in subdued light. For five years I kept transplanting crop after crop without ever sowing again, but in all that time no prothallus was ever known to form a frond whilst in the Wardian case in the subdued light.

Of late years I have used for raising spores five-inch pots covered with flat glasses, and these have been kept plunged an inch deep in water; this has been done because less care is necessary during the earlier period of the germination of the spores. An excess of water does less harm than a defect, for under all circumstances the watering must be from below, as it is all but certain death to water the surface; yet, if the soil is allowed to become dry the developing ferns are destroyed.

In my experience I find no diminution in number of the progeny raised from various varieties of any species, but I differ from the opinion of those who say that hybrid species are equally prolific. It

is true that a few plants have been raised from the hybrid *Polystichum aculeatum* (*cruciatum*), yet I have sown spores from half-a-dozen ferns each year for six years without raising a single plant, and if this hybrid had been even moderately prolific there should now be thousands of plants in existence. Other hybrids, such as *Lastrea remota*, *Asplenium germanicum*, and *Asplenium marinum*, v. *microdon* are to all intents and purposes sterile. This difference in fertility markedly distinguishes a variety from a hybrid species; the progeny of a hybrid species is almost nil.

E. T. LOWE.
Shirenewton Hall, Chepstow.

THE DISTRIBUTION OF LATICIFEROUS TISSUE IN THE LEAF.—In the autumn of 1886, Mr. L. A. Boodle and Miss A. Calvert, who were then working with me as research students, undertook, by my advice, an investigation of the course of the laticiferous tubes in the leaves of plants belonging to various natural orders. Our object was especially to test the accuracy of Haberlandt's view that the laticiferous tubes serve as conductors of assimilated food-material, a view on which doubt had already been cast by the observations of Schimper. Mr. Percy Groom's paper 'On the Functions of Laticiferous Tubes,' in No. x. of the Annals of Botany, has suggested to me that a short summary of the results obtained, though not leading to any very positive conclusions, may be worth publication. The observations were made on sections, both transverse and superficial. The following account is taken, with only verbal alterations, from notes which I made at the time.

Euphorbiaceae.

Euphorbia cotinifolia. Laticiferous cells run in immediate contact with the spongy parenchyma, occasionally sending out branches between its cells.

Other cells or their branches very constantly occur in close contact with the palisade parenchyma. Some branches of the cells run immediately below the epidermis of both surfaces of the leaf, and in some

cases penetrate between the epidermal cells, and may even reach their free surface.

Observations of my own on the leaves of *Manihot Glaziovii* show that only very short branches are given off by the laticiferous tubes (here of course vessels) which accompany the bundles.

Artocarpeae.

Ficus Cooperi. The epidermis is here either one or two cells in thickness. The laticiferous cells constantly send out branches which pass up to and between the chlorophyll-containing cells of the mesophyll. The ends of these branches often reach the epidermis, and where the latter is two cells thick, may penetrate between the cells of the inner layer, and reach the outer. The cell-walls of the outer epidermal layer are sometimes much indented by the ends of the laticiferous cells. The latter reach the epidermis on both surfaces, but more often on the upper than on the lower surface. In the veins, where there is no assimilating tissue, the laticiferous cells also reach the epidermis, but no endings of branches were found here.

Converging palisade cells, similar to those shown by Haberlandt, sometimes occur, but it does not appear that they converge towards laticiferous cells.

F. bengalensis. The upper epidermis is three cells thick. Branches of the laticiferous cells penetrate between the palisade cells to the epidermis, and then between the cells of the latter, sometimes even reaching the cuticle. Most of these branches run approximately at right angles to the surface, but this is not always the case. Here also the laticiferous cells run more frequently to the upper than to the lower surface.

F. elastica. The laticiferous cells penetrate the epidermis on both sides of the leaf. They apparently spread more in the epidermis and in the spongy parenchyma than in the palisade tissue.

The relation of the palisade cells to the collecting-cells ('Sammelzellen' of Haberlandt) was well shown.

F. religiosa. Here the epidermis is only one cell in thickness on both sides of the leaf. Laticiferous cells occasionally reach the epidermis.

F. retusa. The epidermis of both surfaces is two cells thick. Laticiferous cells often reach the epidermis, and occasionally penetrate to

the cuticle, on both sides of the leaf. In other cases a laticiferous cell runs longitudinally along the base of a series of 'collecting cells.' The latter cells are often rich in tannin. In some cases palisade cells were found converging towards a laticiferous cell, as shown by Haberlandt.

F. infectoria. Here tannin sacs are much more abundant, and laticiferous tissue less so, than in other species examined. No relation of the latter to the assimilating tissues could be made out.

The results obtained in this genus were summed up as follows :— No *constant* relation between assimilating and laticiferous tissue, such as is maintained by Haberlandt, was found. On the other hand, in isolated cases arrangements quite like those figured by him were met with. In these leaves the laticiferous cells appear to traverse all tissues equally.

Lobeliaceae.

In *Siphocampylus*, sp. laticiferous vessels were found immediately below the epidermis of the leaf, but were not observed to penetrate it[1].

Compositae.

In *Hypochaeris radicata* the laticiferous vessels accompany the phloem of the bundles, and their branches were not found to penetrate far into the mesophyll.

Aroideae.

In *Alocasia*, sp. no relation could be traced between the laticiferous vessels and the assimilating tissue of the leaf.

In *Xanthosoma*, sp. branches are in many cases given off from the laticiferous vessels, which reach the assimilating tissue, and often penetrate to the epidermis.

The observations were not carried further, as they did not promise to lead to any definite physiological results. Fragmentary as they are, they may serve to supplement and confirm the statements of Professor Schimper and Mr. Groom.

In the case of *Ficus* I have regarded the 'aqueous tissue' as forming part of the many-layered epidermis.

[1] Cf. De Bary, Comp. Anat., Eng. ed., p. 434.

It seems most probable that the laticiferous tubes are related functionally, as well as anatomically, to the secretory sacs of other plants. The exact distribution of the branches is, I think, largely determined by their following the line of least resistance during their sliding growth between the surrounding elements.

All necessary references to the literature of the subject will be found in Mr. Groom's paper.

D. H. SCOTT, South Kensington.

BOTANICAL NECROLOGY FOR 1889.

In preparing the Necrology the Editors have been greatly assisted by Mr. George Murray, of the Botanical Department, British Museum.

CHURCHILL BABINGTON[1]. Born at Roecliffe, Leicestershire, March 11, 1821. Died at Cockfield, Suffolk, January 12, 1889. Educated at the University of Cambridge. M.A. 1846; D.D. 1875; Fellow of St. John's College, 1846. Clergyman. Disney Professor of Archaeology, University of Cambridge, 1865–1880. Biographical notice by Babington in Journal of Botany, 1889, and by Taylor in Trans. Bot. Soc. Edin. XVII (1889). Published:—

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[1] The Editors are indebted to Mr. F. V. Dickens, of London, to Prof. Babington, of Cambridge, and to Mr. J. Bass Mullinger, of St. John's College, Cambridge, for information about Prof. Churchill Babington.

JOHN BALL[1]. Born at Dublin, August 20, 1818. Died at London, October 21, 1889. Educated at Oscott and Christ's College, Cambridge. Barrister. Assistant Poor Law Commissioner, 1846 and 1849. M.P. for Carlow, 1852–1857. Under Secretary of State for the Colonies, 1855–1857. Editor of 'Peaks, Passes, and Glaciers.' First President of Alpine Club. Biographical Notices by Thiselton Dyer in Journal of Botany, 1889, and by Sir Joseph Hooker in Proceedings Royal Geographical Society, Vol. XII. No. 2, February 1890. Published :—

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[1] The Editors are indebted to Sir Joseph Hooker for information about Mr. Ball.

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MILES JOSEPH BERKELEY. Born at Biggin near Oundle, 1803. Died at Sibbertoft, Market Harborough, 30th July, 1889. Educated at Rugby and Christ's College, Cambridge. Clergyman. Curate at Margate; Rector of King's Cliffe, Wansford; Vicar of Sibbertoft, Market Harborough, 1868. Editor of Journal of the Royal Horticultural Society, 1866–1877. Co-editor of Micrographic Dictionary. Biographical notice by Baker in Nature, 1889; by Murray in Journal of Botany, 1889; and by Druce and Taylor in Northamptonshire Notes and Queries, 1889. Published:—

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TITUS CHALUBINSKI.[1] Born at Chociwek, near Radom (Russ. Poland), 1820. Died at Zakopany (Austr. Gallicia), 7 November, 1889. Educated at the Gymnasium of Radom; the Medical Academy of Vilna, 1838–40; the Universities of Dorpat (Russia), 1840–42, and Würzburg, 1842–43. M.D. Physician at the hospital of Warsaw, 1847–57; Clinical Professor at the Medico-surgical Academy, 1852–60; the high School, 1860–69; and the University of Warsaw, 1869–70. Biographical notice by Luczkiewicz in 'Biblioteka Warszawskoi', Dec. 1889; by Turkiewicz in 'Wszechswiat,' Warsaw, 1889, No. 46, etc. Published:—

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ERNEST SAINT-CHARLES COSSON.[2] Born at Paris, July 22, 1819. Died at Paris, December 31, 1889. M.D. 1847. Membre de la Commission Scientifique de l'Algérie, 1852. Président de la Commission Scientifique de la Tunisie, 1882. Officier de la

[1] The Editors are indebted to Prof. Fischer de Waldheim, of Warsaw, for information about Prof. Chalubinski.

[2] The Editors are indebted to M. Malinvaud, of Paris, and Prof. Flahault, of Montpelier, for information about Dr. Cosson.

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KARL DESCHMANN[1]. Born at Idria, January 3, 1821. Died at Laibach, March 11, 1889. Educated at Normal School in Laibach, Gymnasium of Salzburg, and University of Vienna. Curator of the Carniolian Natural History Museum, 1852–1889. Conservator für Kunst- und Historische Denkmale. Biographical notice by Prof. W. Voss in Oesterreichische botanische Zeitschrift, XXXIX (1889). Published:—

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HERMANN THEODOR GEYLER[2]. Born at Schwarzbach, June 15, 1834. Died at Frankfurt am Main, March 22, 1889. Educated at Gymnasium of Weimar and the Universities of Leipzig and Jena. Ph.D. 1860. Private Assistant to Prof. Cramer in Zürich, 1864–7; Teacher of Botany in the Senckenberg Medical Institute, Frankfurt a. M., 1867–89; Curator of

[1] The Editors are indebted to Prof. Dr. Paulin, of Laibach, for information about K. Deschmann.

[2] The Editors are indebted to Dr. Jännicke, of Frankfurt, and Prof. Magnus, of Berlin, for information about Dr. Geyler.

the Museum in the Senckenberg Institut; Director of the Botanic Garden, Frankfurt a. M., 1876–89; Co-editor of Just's Jahresbericht, 1883–9. Biographical notices by Askenasy in Berichte der deutschen botanischen Gesellschaft, Generalversammlungs Heft, 1889; and by Kinkelin in Leopoldina, June, 1889. Published:—

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FERDINAND HAUCK[1]. Born at Brünn, April 29, 1845. Died at Trieste, December 21, 1889. Educated at Gymnasium and Realschule of Brünn, and the High School of Technology of Brünn. Hon. Ph. D., Zürich. Official of the Post Office at Trieste, 1866–89. Biographical notices by S. Z. in Oesterreichische botanische Zeitschrift, 1887; and by Richter in Hedwigia, 1890. Published:—

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KARL FRIEDRICH WILHELM JESSEN[2]. Born at Schleswig, September 15, 1821. Died at Berlin, September 15, 1889. Educated at the University of Kiel. Professor in Agricultural

[1] The Editors are indebted to Dr. Marchesetti, of Triest, and to Dr. Paul Richter, of Leipzig, for information about Dr. Hauck.

[2] The Editors are indebted to Prof. Magnus, of Berlin, and to Prof. Schmitz, of Greifswald, for information about Prof. Jessen.

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WILLIAM ALLPORT LEIGHTON[1]. Born at Shrewsbury, 7th May, 1805. Died at Luciefelde, Shrewsbury, 25th February, 1889. Educated at Mr. George Case's private school, Shrewsbury; and Free Grammar School, Wolverhampton; and University of Cambridge. Clergyman. Curate of Holy Trinity and St. Giles'

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LEO LESQUEREUX[1]. Born at Fleurier, Neuchatel, November 18, 1806. Died at Columbus, Ohio, October 25, 1889. Educated at Academy and College of Neuchatel, 1821–1827. Teacher of French in Germany, 1827–1829. Principal of the College of La Chaux de Fonds, Neuchatel, 1829. Went to America, 1848. Employed by Sullivant, Gray, Agassiz, and the U.S. Geological Survey. Biographical notice by Barnes, in the Botanical Gazette, XV (1890). Published:—

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SEXTUS OTTO LINDBERG[1]. Born at Stockholm, March 29, 1835. Died at Helsingfors, February 20, 1889. Educated at Stockholm and the University of Upsala. M.D. 1865. Teacher of Natural History and Pharmacognose in the Pharmaceutical Institution of Stockholm, 1862–65; Professor of Botany and Director of the Botanic Garden, Helsingfors, 1865–1889. Biographical notice in Botaniska Notiser, 1889; and by Saelan in Meddelanden of Societas pro Fauna et Flora fennica, XVI; and by Norrlin in Acta Societatis scientiarum Fenniae, 1890. Published:—

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WILLIAM RAMSAY MACNAB. Born at Edinburgh, November, 1844. Died at Dublin, December, 1889. Educated at the Edinburgh Academy, and Universities of Edinburgh and Berlin. M.D. 1866. Assistant Physician Crichton Royal Institution, Dumfries, 1867–1870. Professor of Natural History in the Royal Agricultural College, Cirencester, 1870–1872. Professor of Botany, Royal College of Science, Dublin, 1872–1889. Scientific Superintendent, Glasnevin Botanic Garden, 1880–89. Swiney's Lecturer on Geology, 1887–89 Biographical notice in Nature, 1889, and in Journal of Botany, 1890. Published:—

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CHARLES FRÉDÉRIC MARTINS[1]. Born at Paris, February 6, 1806. Died at Paris, March 7, 1889. Educated at Lycée Charlemagne, Paris, and the Universities of Geneva and Paris. Agrégé d'Histoire Naturelle in the Faculté de Médecine, Paris, 1839. Assistant to and afterwards Substitute Professor of Botany for Achille Richard at the Faculté de Médecine, Paris; also Substitute Professor of Geology for Constant Théorst at the Sorbonne. Professor of Botany and Natural History in the Faculté de Médecine and Director of the Botanic Garden at Montpellier, 1831. Emeritus, 1879. Correspondant de l'Institut, 1863. Biographical notice by Blanchard in Progrès Médical, sér. 2, T. X (1889); in Gazette hebdomadaire de Médecine et Chirurgie, sér. 2, XXVI (1889); by Magnus in Leopoldina, XXVI (1890). See also Titres et Travaux de M. Ch. Martins, 8vo; and Flahault in L'Institut de Botanique, Montpellier, 1890. Published:—

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GIUSEPPE MENEGHINI[1]. Born at Padova, July 30, 1811. Died at Pisa, January 29, 1889. Educated by Abate Giuseppe Bernardi and Pietro Melo, and at the University of Padua. M.D. 1834. Assistant to the Professor of Botany at the University of Padua, 1834–38. Professor of the Science Faculty, University of Padua, 1838–49. Professor of Physical Geography

[1] The Editors are indebted to Professor Arcangeli for information regarding Professor Meneghini.

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MARY PHILADELPHIA MERRIFIELD (Mrs.). Born at London, 15th April, 1804. Died at Stapleford, Cambridge, 4th January, 1889. Biographical notice in Journal of Botany, 1889. Published:

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JOSEPH-ANTOINE MOUGEOT. Born at Bruyères (Vosges), May 8, 1815. Died at Bruyères, February 20, 1889. Educated at the University of Strasbourg. M.D. 1837. Physician in the Hospital of Bruyères. Mayor of Bruyères, 1854–55, 1861–68, 1871–76. Member and President of the Conseil Général des Vosges 1859–79. Chevalier of the Legion of Honour. Biographical notice by Roumeguère in Bulletin de la Société Mycologique de France, V (1889). Published:—

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LOUIS-FRANÇOIS PERROUD[1]. Born at Lyons, February 24, 1833. Died at Lyons, February 26, 1889. M.D., Paris, 1858. Physician. Professor-adjoint of the Faculty of Medicine of Lyons. Biographical notices by Lépine in Lyon Médical, March 10, 1889; and by Gayet in La Province Médicale de Lyon, March 2, 1889. Published:—

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And many articles on Medical Subjects.

SAVA PETROVIČ[2]. Born at Shabatz, Serbia, January 14, 1839 (old style). Died at Belgrade, January 20, 1889 (old style). Educated at Shabatz, the High School of Belgrade, and Faculté

[1] The Editors are indebted to Dr. Beauvisage, of Lyons, for information regarding Dr. Perroud.

[2] The Editors are indebted to Professor Nedich, of Belgrade, for information about Dr. Petrovič.

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JOHANN JOSEPH PEYRITSCH. Born at Völkermarkt, Carinthia, October 25, 1835. Died at Gries, near Bozen, March 14, 1889. Educated at Gymnasium and Johanneum of Graz, and the Polytechnic Institute of Vienna. M.D. 1860. Naval Surgeon, 1864–1870. Curator of K. K. botanische Hof- Cabinet in Vienna, 1871–1878. Docent in the University of Vienna, 1873–1878. Professor of Botany in the University, and Director of the Botanic Garden of Innsbruck, 1878–1889. Biographical notice by Kronfeld in Botanisches Centralblatt, XI (1889), and by Heinricher in Berichte der deutschen botanischen Gesellschaft, Generalversammlungs Heft, 1889. Published:—

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HEINRICH GUSTAV REICHENBACH.[1] Born at Dresden, Jan. 3, 1824. Died at Hamburg, May 6, 1889. Educated at the Gymnasium, the Medical Academy at Dresden, 1835–1844, and the University of Leipzig, 1844–1847. Ph. D. 1852. Deputy-Professor of Natural History at the Forestry and Agricultural Academy of Tharand, 1848–1853. Privat Docent at Leipzig, 1852–1855. Extraordinary Professor and Curator of Herbarium of University of Leipzig, 1852–1855. Lecturer on Botany and Zoology at the Agricultural Institution of Lütschena, 1854. Co-editor of Pescatoria, 1854. Professor of Natural History at the Gymnasium and Director of the Botanic Garden at Hamburg, 1863–1889. Biographical notice by Britten in Journal of Botany, 1889; in Gardeners' Chronicle, 1889; in Garten-Flora, 1889; by Dilling in Jahrbuch der Hamburgischen Wissenchaftlichen Anstalten, VII (1890). Published:—

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In addition to the above Reichenbach published an enormous number of papers and notices of varying length containing descriptions of species and monographs of genera of Orchids, and a few relating to plants of other families beginning in the year

[1] The Editors are indebted to Dr. Masters, of London, and to Dr. Beck, of Vienna, for information regarding Professor Reichenbach.

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EDUARD KARL LUDWIG PFEIL SCHNEIDER[1]. Born at Sudenburg, Magdeburg, June 26, 1809. Died at Schönebeck, February 9, 1889. Educated at the Gymnasium of the Kloster Unserer Lieben Frau, Magdeburg, and the Universities of Berlin and Jena; 1834 Auscultator; 1840 Referendar; 1843–1856 Bürgermeister (Mayor) of Schönebeck; 1847 Member of the Vereinigte Landtag; 1848 of the National Versammlung; 1849 of the Second Chamber; 1861–1866 of the House of Deputies; 1864–1869 Stadtverordneter (member of the Town Council), at Berlin. Biographical notices by Ebeling, Jahresber. u. Abhandl. Naturw. Vereins in Magdeburg (1889); P. Ascherson in Verh. Bot. Ver. Brandenburg, XXXI (1889). Published:—

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SEBASTIAN VIDAL Y SOLER. Born at Barcelona, April 1, 1842. Died at Manila, July 28, 1889. Educated at Barcelona and the School of Forestry Villaviviosa de Odosa. Engineer, Director of the Botanic Garden in Manila; Inspector General of Forests in Philippine Islands. Published:

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[1] The Editors are indebted to Professors Ascherson and Magnus, of Berlin, for information about Dr. Schneider.

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ERNST RUDOLPH VON TRAUTVETTER[1]. Born at Mitau, February 20, 1809. Died at St. Petersburg, January 24, 1889. Educated at the Gymnasium of Mitau, and the Universities of Dorpat and Königsberg. Assistant Director of the Botanic Garden of Dorpat, 1833. Docent at the University of Dorpat, 1834. Assistant Director of the Imperial Botanic Garden at St. Petersburg, 1835–1838. Professor of Botany at the University of Kieff, and Director of the Botanic Gardens at Kremeniez and Kieff, 1838–1859. Director of the Agricultural School at Gori-Ghorki, 1860–1862. Director of the Imperial Botanic Garden at St. Petersburg, 1863–1875. Biographical notices by Regel in Acta Horti Petropolitani, XI, and by Von Herder in Botanisches Centralblatt, XXXVIII (1889). Published:—

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———— : Etiologie des maladies parasitaires à propos de quelques Epiphyties observées récemment en Lorraine.

FLICHE : Influence de l'humidité fraîche sur la végétation forestière sur les bords du lac de Côme.

MONNIER : Sur la valeur morphologique de l'albumen chez les Angiospermes.

———— : Constitution des ovaires uniloculaires à placentas pariétaux multiples.

FLICHE : Sur la Faune et la Flore de quelques tufs quaternaires du nord-est de la France.

Bulletins de la Société des Sciences Naturelles de Saone-et-Loire. Tome IV.

Fasc. 2. BIGEARD : Notes sur la Flore des Vallées de la Brenne et du Doubs dans le canton de Pierre.

„ — QUINCY : Notes botaniques sur Uchon et ses environs.

„ 3. ———— : Note sur les Champignons phosphorescents.

Bulletin de la Société d'Histoire Naturelle de Savoie. 1888.

No. 1. RÉVIL : Les Algues fossiles.

„ 2. FAVRE : La dispersion des plantes.

Bulletin de la Société Géologique de France. Série 3. Tome XVI.

No. 8. ZEILLER : Sur la présence, dans le grès bigarré des Vosges, de l'*Acrostichides rhombifolius*, Fontaine.

Bulletin de la Société Linéenne de Normandie. Série. Vol. II.

MORIÈRE : Note sur un échantillon de *Williamsonia*.

DANGEARD : Recherche sur la structure des Salicornieae et des Salsolaceae.

LIGNIER : Note relative à des protubérances observées sur des branches de *Biota*.

TOPSENT : Note sur la formation des anthérozoides dans l'*Eudora elegans*.

DANGEARD : Anatomie et dévelloppement de l'*Eranthis hyemalis*.

MALINVAUD : *Ranunculus choerophyllos* et *flabellatus*.

TOPSENT : Sur deux nouvelles espèces de *Chytridium*.

Bulletin de la Société Mycologique de France. Tome IV. Fasc. 2.

PATOUILLARD ET GAILLARD : Champignons du Vénézuela et principalement de la région du Haut-Orénoque (Pl. VI–XIII).

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ROLLAND : Trois nouvelles espèces de Discomycètes (Pl. XV).

PRILLIEUX : Productions de périthèces de *Physalospora Bidwellii* au printemps sur les grains des raisins attaqués l'année précédente par le Black Rot.

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DUFOUR : Rescherches sur le contenu en eau de deux variétés du *Psalliota campestris*.

PATOUILLARD : Note sur trois espèces mal connues d'Hyménomycètes.

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PATOUILLARD : Le Genre *Ganoderma*.

Bulletin de la Société Philomathique de Paris. Série 7. Tome XII.

No. 3. FRANCHET : La végétation de l'île d'Yéso et diagnoses d'espèces nouvelles du Japon (*continued*).

„ 4. ———— : Note sur les *Cypripedium* de la Chine Occidentale.

Bulletin Mensuel de la Société Linnéenne de Paris.

No. 95. BAILLON : Sur les Schizophytes des urines acides, puis alcalines.

„ — PIERRE : Sur le genre *Telotia*, n. gen. (Ménispermacées).

„ — BAILLON : Organogénie ovulaire des *Acokanthera*.

Bulletin Mensuel de la Société Linnéenne de Paris (*continued*).

No. 95. BAILLON: Sur l'organisation florale de quelques Gentiancées (*continued*).
„ — ———: Types nouveaux d'Apocynacées (*continued*) (continued in No. 97).
„ 96. ———: Sur un mode particulier de propagation du Mildew.
„ — ———: Remarques sur le genre *Thenardia*.
„ — ———: Sur le *Dissolaena verticillata*, Lour.
„ — PIERRE: Sur le genre *Melientha*.
„ 97. ———: Sur l'*Harmandia*, n. gen. (Olacées).
„ — DURAND: Note sur l'organogénie du *Poa annua*.
„ — BAILLON: Les stipules et les bractées des Circées.
„ — ———: Sur quelques *Gynopogon* néo-calédoniens.

Bulletin Scientifique de la France et de la Belgique (Giard). Paris.

Nos. 4–8.
GIARD: Sur quelques Entomophthorées.
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HUTH: Sur la convergence dans les règnes animal et végétal.
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„ — LOEWENTHAL: Expériences biologiques et thérapeutiques sur le choléra.
„ — HECKEL: Sur quelques particularités structurales des ascidies et sur l'organogénie des feuilles ascidiformes du *Sarracena Drummondii*, Croom.
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„ — RAULIN: Action de divers phosphates sur la culture des Céréales.
„ — VIOLLETTE ET DESPREZ: Races de betteraves hâtives et races tardives.
„ — GUIGNARD: Formation des anthérozoides des Characées.
„ 2. TANRET: Nouveau principe immédiat de l'ergot de seigle, l'ergostérine.
„ — HECKEL ET SCHLAGDENHAUFFEN: Sur la constitution chimique et la valeur industrielle du latex concrété de *Bassia latifolia*, Roxb.
„ — DAGUILLON: Sur le polymorphisme foliare des Abiétinées.
„ 4. LOEWENTHAL: Virulence des cultures du bacille cholérique et l'action que le Salot exerce sur cette virulence.
„ — PEUCH: Passage du bacille de Koch dans le pus de séton des sujets tuberculeux.
„ 5. SCHLOESING: Déperdition d'azote pendant la décomposition des matières organiques (continued in No. 6).
„ — TREUB: Sur le Jardin botanique et le laboratoire de Buitenzorg.
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„ 6. FLOT: Sur la région tigillaire des arbres.

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„ — GRANEL : Observations sur les suçoirs de quelques Rhinanthées.

„ 8. CHAUVEAU : Les microbes ci-devant pathogènes, n'ayant conservé, en apparence, que la propriété de végéter en dehors des milieux vivants, peuvent-ils récupérer leurs propriétés infectieuses primitives?

„ — GIRARD : Recherches sur la culture de la pomme de terre industrielle (continued in Nos. 10 and 12).

„ 9. ARLOING: Effets généraux des substances produites par le *Bacillus heminecrobiophilus* dans le milieux de culture naturels et artificiels.

„ — GUIGNARD : Sur la formation des anthérozoïdes des Hépatiques, des Mousses et des Fougères.

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„ — HARTOG : Recherches sur la structure des Saprolégniées.

„ 14. BERTHELOT : Fixation de l'azote par la terre végétale nue, ou avec le concours des Légumineuses.

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„ — PRUNET : Sur les faisceaux foliaires.

„ — MICHON : Sur le topinambour obtenu de semis.

„ 17. DEHERAIN : Pertes et gains d'azote constatés au champs d'expériences de Grignon de 1875 à 1889.

„ — GRAND' EURY : Développement souterrain, semences et affinités des Sigillaires.

„ — MUNTZ ET MARCANO : Sur la formation des terres nitrées.

„ — MUSSET : Mouvements spontanés du style et des stigmates du Glaïeul (*Gladiolus segetum*).

„ — RODIER : Sur la formation et la nature des sphéro-cristaux.

„ 18. CHARDONNET : Sur une soie artificielle.

„ 20. MUNTZ ET MARCANO : Sur la proportion de nitrates contenus dans les pluies des régions tropicales.

„ — RENAULT : Sur un nouveau genre fossile de tige Cycadéene.

„ 21. TRÉCUL : Sur la nature radiculaire des stolons des *Nephrolepis*. Réponse à M. Van Tieghem.

„ — GRAND' EURY : Calamariées : *Arthropitus* et *Calamodendron*.

„ — LABOULBÈNE : Sur les dégâts produits sur les épis de maïs par un insecte hémiptère (*Pentatoma viridula*, L.).

Comptes Rendus hebdomadaires de la Société de Biologie. Série 9, Tome I.

No. 1. LATASTE : Qu'est-ce que l'être vivant ? Définition nouvelle.
„ — JUMELLE : Influence du ralentissement de l'assimilation sur la transpiration chlorophyllienne.
„ 2. GILBERT ET LION : Note sur un microbe trouvé dans un cas d'endocardite infectieuse.
„ — CAPITAN ET MORAU : Recherches sur les micro-organismes de l'estomac.
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„ — JUMELLE : Etude physiologique de la végétation à l'obscurité.
„ 11. GALIPPE ET VIGNAL : Note sur les micro-organismes de la carie dentaire.
„ 12. REGNARD : Note à propos de la pression exercée par les graines qui se gonflent.
„ 14. SABLON : Expériences sur l'absorption de l'eau par les graines.
„ 19. GRÉHANT : Pression exercée par les graines de lupin placées dans un courant d'eau.

L'Illustration Horticole. Tome XXXVI contains plates and descriptive notice of *Passiflora Watsoniana*, M. T. Mast; *Persea gratissima*, Gaertn.; *Oxera pulchella*, Labill.; *Cypripedium* × *Maesereelianum*, Hort.; *Impatiens Rodigasi*, L. Lind.; *Odontoglossum crispum*, Lindl., var. *président Zhaldua*; *Clivia miniata*, var. *Chevalier Hynderick*; *Cypripedium barbatum*, Lindl., var. *Warnerianum*; *Anthurium Scherzerianum*, Schott, var.

Journal de Botanique. 3e Année.

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„ — SAUVAGEAU : Sur la racine du *Najas*.
„ — FRANCHET : Note sur le *Ranunculus chaerophyllos*, L.
„ 2. MASCLEF : Note sur le *Daucus hispidus*, DC.
„ — PATOUILLARD : Fragments mycologiques (continued in No. 3).
„ — MALINVAUD : *Ranunculus chaerophyllos*, L.
„ — Note sur le *Vicia villosa*, Roth.
„ — Nouvelle méthode pour reconnaître de petites quantités d'invertine.
„ 3. DOULIOT : Recherches sur le Périderme.
„ — MASCLEF : Etudes sur la géographie botanique du nord de la France (continued in No. 6).
„ 4. FRANCHET : Observations sur deux *Primula* à graines anatropes.
„ — MER : Influence de l'exposition sur l'accroissement de l'écorce des Sapins (continued in Nos. 5–8).
„ — COSTANTIN : *Tulasnella, Protrotremella, Pachysterigma*.
„ — SAUVAGEAU : Contributions à l'étude du système mécanique dans la racine des plantes aquatiques; les *Potamogeton*.
„ 5. CASTILLO : Contribution à la flore de l'Amérique équatoriale.
„ — VUILLEMIN : Sur les affinités des Frankéniées.
„ 6. CAMUS : Note sur des Orchidées des environs de Paris × *Orchis Luizetiana*, n. hyb.

Journal de Botanique (*continued*).

No. 7. FRANCHET : *Nomocharis*, nouveau genre de Liliacées-Tulipées.
„ — DOULIOT : Influence de la lumière sur le développement du liège.
„ 8. MAURY : Enumeration des plantes du Haut-Orénoque récoltées par MM. J. Chaffanjon et A. Gaillard (continued in Nos. 9 and 11).
„ 9. GRANEL : Recherches sur l'origine des suçoirs des Phanérogames parasites.
„ — HARIOT : Liste des Algues recueillies à l'île Miquelon par M. le docteur Delamarre (continued in Nos. 10 and 11).
„ 10. PATOUILLARD : Fragments mycologiques.
„ — SAUVAGEAU : Contribution à l'étude du système mécanique dans la racine des plantes aquatiques ; les *Zostera*, *Cymodocea*, et *Posidonia*.
„ — SABLON : Note sur les suçoirs des plantes parasites.
„ 11. LAGERHEIM : Sur un nouveau genre d'Urédinées.
„ — GARCIN : Sur le pigment de l'*Euglena sanguinea*, Ehrb.

Journal de Micrographie. 1889.

No. 1. SMITH : Contribution à l'histoire naturelle des Diatomacées (*continued*) (continued in Nos. 2–4).
„ — GIARD : Note sur deux types remarquables d'Entomophthorées.
„ 6. GUIGNARD : Développement et constitution des Anthérozoides des Fucacées.
„ — BONARDI : Sur les Diatomées de lac d'Idro (continued in No. 7).
„ 8. ROUX : De la Microbiologie dans la prophylaxie des maladies infectieuses.
„ — RODIER : Sur la formation et la nature des sphéro-cristaux.
„ — HARTOG : Recherches sur la structure des Saprolégniées.
„ 9. PRUNET : Sur les faisceaux foliaires.
„ — PERAGALLO : Note sur quelques Diatomées saumâtres du Médoc.

Journal de Pharmacie et de Chimie. 1889. Tome XIX.

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„ 4. FRAGNER : Sur un nouvel alcaloide, l'impérialine (from the bulbs of *Fritillaria imperialis*).
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„ — HECKEL ET SCHLAGDENHAUFFEN : Sur un latex du *Bassia latifolia*.
„ 8. BOURQUELOT : Recherches sur les matières sucrées de quelques espèces de Champignons.
„ 9. BERTHELOT : Sur la fixation de l'azote dans les oxydations lentes.
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L'Orchidophile. 9e Année.

No. 92. ROLFE : *Epidendrum stenopetalum*.
„ — BERGMAN : Les Orchidées de semis (continued in Nos. 93–97 bis).
„ — Les *Anaectochilus*.
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Mémoires de l'Académie des Sciences, Belles-lettres et Arts de Lyon. XXIX.

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Revue Bryologique. 1889

No. 1. Philibert: Etudes sur le péristome (*continued*).
„ — Renauld et Cardot: Notice sur quelques mousses de l'Amérique du Nord.
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„ — ———: Notice sur une Mycose du sporange des Mousses.
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„ — Corbière: *Weisia Alberti*, n. sp.
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„ — BONNIER: Etudes sur la végétation de la vallée de Chamounix et de la chaîne du Mont Blanc.
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„ — SABLON: Revue des Travaux d'Anatomie publiés en 1888. I. Anatomie cellulaire.
„ 2. ROSENVINGE: Influence des agents extérieurs sur l'organisation polaire et dorsiventrale des plantes (continued in Nos. 3–6).
„ — GUIGNARD: Développement et constitution des Anthérozoïdes (*continued*). II and III. Muscinées et Fougères.
„ — PLANTA: Note sur la composition des Tubercules de Crosne du Japon (*Stachys tuberifera*).
„ — SABLON: Revue des Travaux d'Anatomie publiés en 1888 (*continued*). II. Anatomie des tissus. III. Anatomie appliquée à la classification. IV. Variétés.
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„ 3. JUMELLE: Recherches physiologiques sur le déve oppement des plantes annuelles (continued in Nos. 4–6).
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No. 41. BARBICHE: Note sur l'*Omphalia retosta*, Fr., v. *Lotharingiae*.
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„ — PATOUILLARD: Le genre *Coleopuccinia*.
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„ — DUDLEY: Les Champignons destructeurs du bois (Tab. LXXIV).
„ — Fungi nonnulli Paraguariae et Fuegiae auctore Spegazzini.
„ — LAGERHEIM: L'acide lactique excellent agent pour l'étude des Champignons secs.
„ — Fungi quidam novi vel minus bene cogniti auctore Karsten.
„ — MARTELLI: Sur la phosphorescence de l'*Agaricus olearius*, DC.

Revue Scientifique du Bourbonnais (E. Olivier). Moulins. 1889.

No. 3. GONOD-D'ARTEMARE: Matériaux pour la flore d'Auvergne.
„ 5. DUMAS-DAMON: Bryologie du Puy-de-Dôme.
„ — GAY: Contribution à l'histoire de la Flore bourbonnaise.
„ 6. BUFFAULT: La forêt de Lespinasse (avec Carte).

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———— : Reliquiae Rutenbergianae, VIII. Botanik (*concluded*) (Taf. VI.)

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AHRENS: Die Alkaloïde der Mandragora.

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HEIDEN: Beitrag zur Algenflora Mecklenburgs.

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Archiv für die gesammte Physiologie des Menschen und der Thiere. Pflüger. Bd. 45.

Heft 1 und 2.

VERWORN: Die polare Erregung der Protisten durch den galvanischen Strom (Taf. I u. II).

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Berichte der deutschen botanischen Gesellschaft. Bd. VII.

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„ — Ambronn: Das optische Verhalten und die Structur des Kirschgummis.

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„ — Palladin: Kohlehydrate als Oxydationsprodukte der Eiweissstoffe.

„ — Hellriegel und Wilfarth: Erfolgt die Assimilation des freien Stickstoffs durch die Leguminosen unter Mitwirkung niederer Organismen?

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„ — Müller: Durchbrechungen der Zellwand in ihren Beziehungen zur Ortsbewegung der Bacillariaceen (Taf. VII).

„ — ——— : Auxosporen von *Terpsinoë musica*, Ehr. (Taf. VIII).

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„ 5. Reiss: Ueber die in den Samen als Reservestoff abgelagerte Cellulose und eine daraus erhaltene neue Zuckerart, die 'Seminose.'

„ — Bauer: Ueber eine aus Laminariaschleim entstehende Zuckerart.

„ — Fischer: Ueber Harmin und Harmalin (Alkaloids of *Peganum harmala*).

„ — Hesse: Zur Kenntniss der Cocabasen.

„ — Liebermann: Zur Geschichte der Cocabasen.

„ 7. Wheeler und Tollens: Ueber die Xylose (Holzzucker) und das Holzgummi.

„ — Washburn und Tollens: Ueber Mais und Gewinnung von krystallisirtem Rohrzucker aus demselben.

„ — Crampton: Borsäure als Bestandtheil der Pflanzen.

„ 8. Schulze: Zur Kenntniss der chemischen Zusammensetzung der Pflanzenzellmembranen.

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„ — HANSGIRG: Bemerkungen über einige von S. Winogradsky neulich aufgestellte Gattungen und Arten von Bakterien.
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„ — Wittmack: *Billbergia Windii* hort., Makoy (Abb. 3–5).
„ — Reichenbach, f.: *Grammatophyllum speciosum*, Bl., *Hypericum Moserianum*, n. hybr.
„ 2. Ortgies: *Cattleya Schilleriana*, Reich. f. (Taf. 1290).
„ — Hennings: *Erythrophloeum pubistamineum*, n. sp. (Abb. 8).
„ — Alphabetisches Verzeichniss sämmtlicher im Monat October 1888 beschriebenen neuen oder abgebildeten älteren Pflanzen mit kurzen Beschreibungen.
„ 3. Wittmack: *Billbergia thyrsoidea*, Mart. (Taf. 1291).
„ — Reichenbach, f.: *Odontoglossum vexillarum Leopoldii II*, Rchb. f.
„ — Wittmack: *Colocasia Indica*, Engl. (Abb. 16).
„ — Alphabetisches Verzeichniss sämmtlicher im Monat November 1888 beschriebenen neuen oder abgebildeten älteren Pflanzen mit kurzen Beschreibungen.
„ 4. Wittmack: *Convallaria majalis*, L., var. *prolificans* (Taf. 1292).
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„ — Runge: Zwei neue Cacteen: *Mammillaria Grusoni*, Runge, u. *Echinocactus Bolansis*, Runge (Abb. 20 und 21).
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„ 5. Rössing: *Anthurium Andreanum* u. seine Hybriden (Taf. 1293).
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„ 6. *Scilla Ledieni*, Engl. (Taf. 1294).
„ 7. Lindberg: *Rhipsalis pulvinigera*, Lindley, n. sp. (Abb. 33–35).
„ — Alphabetisches Verzeichniss sämmtlicher im Monat Januar 1889 beschriebenen neuen oder abgebildeten älteren Pflanzen mit kurzen Beschreibungen.
„ 8. Wittmack: *Aërides expansum Leoniae*, Rchb. f. (Taf. 1296).
„ — Hennings: Ueber *Picea Alcockiana* u. *ajanensis* (Abb. 40).

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„ 9. Wittmack: *Hippeastrum reticulatum*, Herb. (Taf. 1297 und Abb. 41).
„ — Köhler: Subtropische Pflanzen im freien Lande (Abb. 42 und 43).
„ — Hafner: Ueber Unfruchtbarkeit mancher Sauerkirschbäume.
„ — Alphabetisches Verzeichniss sämmtlicher im Monat Februar 1889 beschriebenen neuen oder abgebildeten älteren Pflanzen mit kurzen Beschreibungen.
„ 10. Urban: *Simaruba Tulae*, Urb. (Taf. 1298).
„ — Wittmack: *Zizania aquatica*, L., der Wasserreis (Abb. 44–46).
„ 11. St. Paul-Illaire: *Cattleya Walkeriana*, Gardner (Taf. 1299).
„ — Hildmann: *Echinopsis cristata*, Salm. (Abb. 47).
„ — Wittmack: *Tillandsia streptophylla*, Scheidw. (Abb. 48).
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„ — Alphabetisches Verzeichniss sämmtlicher im Monat März 1889 beschriebenen neuen oder abgebildeten älteren Pflanzen mit kurzen Beschreibungen.
„ 12. Regel: *Eucharis Lehmanni*, Rgl. (Taf. 1300).
„ — ———: *Tulipa Dammanni*, Rgl. (Taf. 1300).
„ — Wittmack: *Tigridia Pringlei*, Watson (Abb. 51).
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„ — Dietel: Kurze Notizen über einige Rostpilze.
„ — Hauck: Ueber einige von J. Hildebrandt im Rothen Meere und im Indischen Ocean gesammelte Algen, VI. (*concluded.*)
„ — Karsten: Fungi aliquot novi in Brasilia a Dr. Wainio anno 1885 lecti.
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„ — WITTMACK : Plantae Lehmannianae in Guatamela, Costa Rica, Columbia, Ecuador, etc., collectae. Bromeliaceae.

„ — PAX : Nachträge u. Ergänzungen zu der Monographie der Gattung *Acer*.

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PACHER : In Kärnten wildwachs. Gefässpflanzen.

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„ — KLEIN : Morphologische u. biologische Studien über die Gattung *Volvox*.

„ — KRABBE : Zur Kenntniss der fixen Lichtlage der Laubblätter.

„ 3. RODEWALD : Weitere Untersuchungen über den Stoff- und Kraftumsatz im Athmungsprocess der Pflanze.

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„ — SCHUMANN : Blüthenmorphologische Studien (Taf. XVII).

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BÖHR : Das Vorkommen des Kartoffelkäfers (*Doryphora decemlineata*, Say) in Lohe (Kreis Meppen).

HOFFMEISTER : Beiträge zur Kryptogamenflora der Umgegend Osnabrücks.

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WÜNSCHE : Pilzflora der Umgegend von Zwickau.

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Heft 1. BRIEGER : Zur Kenntniss der Bildung von Ptomainen und Toxinen durch pathogene Bakterien.

„ — SCHWENDENER : Die Spaltöffnungen der Gramineen und Cyperaceen (Taf. I).

„ 3. ——————— : Zur Doppelbrechung vegetabilischer Objecte.

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SCHULTZE : Phanerogamen um Altenburg.

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HAUPTFLEISCH: Zellmembran u. Hüllgallerte der Desmidiaceen.

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WINTER: Am Isteiner Klotze.

KNEUCKER: *Carduus nutans* × *acanthoides*, Koch.

HENNINGS: Zur Technik der Pflanzenconservirung.

Nos. 59, 61.

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STERK: *Corylus glandulosa*, Schuttl.

MAUS: Botanische Wanderungen um Alt-Breisach im Juli u. Aug.

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SCHEUERLE: Die frühblüthigen Weiden.

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GILL: Botanische Miszellen aus der Südsee.

SCHULZE: Die Orchideen der Flora von Jena (Taf. I).

————: *Melica Aschersonii* (*M. nutans* × *picta*).

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IV. RADDE: Pflanzen in der Schneeregion des Kaukasus.

V. RINK: Die neuern dänischen Untersuchungen in Grönland, 1888.

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No. 1. HÖCK: Einige Hauptergebnisse der Pflanzengeographie in den letzen 20 Jahren (continued in Nos. 2, 6, and 7).

„ — HUTH: Giebt es eine Parthenogenesis im Pflanzenreiche?

„ — HÖCK: Ein Sammelplatz aus zwei Floren.

„ 3. ——: Samenschutz bei der Rose von Jericho.

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„ — ——: *Welwitschia mirabilis*.

„ 6. ASCHERSON: Die Verbreitung von *Achillea cartaliginea*, Ledeb., und *Polygonum danubiale*, Kern. im Gebiete der Flora der Provinz Brandenburg.

„ 7. HAGER: Ueber die giftige Wirkung einiger *Lathyrus*-Arten.

„ — HÖCK: Das Anschmiegen der Hochgebirgspflanzen an den Boden.

„ 8. HUTH: Die Verbreitung der Pflanzen durch die Excremente der Thiere (continued in Nos. 9–12).

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„ — ——: Verbreitung der Pflanzen durch die Excremente der Thiere (continued in No. 2).

„ — ——: Insectenfang durch hakige Pflanzenhaare.

„ 2. KOCH: Untersuchungen über die Stickstoffaufnahme der Gramineen u. Leguminoseen.

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No. 1. Borbás : Die Hybriden der pentapetalen Linden.
„ — Sagorski : Plantae criticae Thuringiae, II.
„ — Woerlein : Beiträge inbezug auf die Verbreitung der Potentilla-Arten.
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„ 3. Seemen : Zwei neue Weiden : *Salix Strähleri* u. *S. Schumanniana.*
„ — Sagorski : Plantae criticae Thuringiae : Die in Thüringen beobachteten Bastarde der *Rosa gallica.*
„ — Bornmüller : Zur Flora der Umgebung Leipzigs.

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Wille : Beiträge zur Entwickelungeschichte der physiologischen Gewebesysteme bei einigen Florideen (Taf. III–VIII).

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„ — Hertwig : Ueber Kernstructur u. ihre Bedeutung für Zelltheilung u. Befruchtung.
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„ 3. Buchner : Notiz betreffend die Frage des Vorkommens von Bacterien im normalen Pflanzengewebe.

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No. 1. BUMM : Die Phagocytenlehre u. der *Gonococcus.*

„ 3. LEHMANN : Ueber die Biologie des *Bacterium phosphorescens*, Fischer.

Sitzungberichte der physikalisch-medicinischen Societät zu Erlangen. München, 1888.

HANSEN : Ueber Verflüssigung der Gelatine durch Schleimpilze (title only).

ROSENTHAL : Ueber einen besonderen Nährboden für Bacterien aus Alkalialbuminat.

Sitzungsberichte und Abhandlungen der Naturwissenschaftlichen Gesellschaft Isis in Dresden. 1888. July—Dec.

DRUDE : Die Vegetationsformationen u. Charakterarten im Bereich der Flora Saxonica.

REICHE : Litteratur zur Flora des Königreichs Sachsen aus dem 19. Jahrhundert.

SEIDEL : *Peucedanum aegopodioides* (Taf. II. und III).

Untersuchungen aus dem Kgl. bot. Institute in Münster. Heft VIII.

BREFELD : Untersuchungen aus dem Gesammtgebiete der Mykologie. Fortsetzung der Schimmel- u. Hefenpilze. Heft VIII. Basidiomyceten.

Verhandlungen des Botanischen Vereins der Provinz Brandenburg. XXX.

ASCHERSON : Einige biologische Eigentümlichkeiten der Pedaliaceae.

HENNINGS : Ueber *Oligoporus rubescens*, Bref.

MAGNUS : Fasciation von *Myosotis alpestris.*

————: Ueber einige Pilze aus den Braunkohlengruben bei Fürstenwalde a. Spr. und Frankfurt a. O.

POTONIE : Ueber *Tylodendron.*

SCHULZ : Geschlechtsverteilung bei den Umbelliferen.

HOFFMANN : Vaterland und Auffindung der Orchideen- Gattung *Orestia*, Ridl.

DAMMER : Ueber einige Fichtenformen.

JACOBASCH : Ueber Formen von *Papaver Rhoeas* und *Collybia stipitaria.*

WITTMACK : Ueber den Kronenapfel.

ASCHERSON : Adventivpflanzen der Oelfabrik in Mannheim.

MEZ : Morphologische Studien über die Familie der Lauraceen.

MITTMANN : Beiträge zur Kenntniss der Anatomie der Pflanzenstacheln (Taf. I und II).

WINKLER : *Chenopodium album forma microphyllum*, Coss. et Germ. in der Provinz Brandenburg.

BECKMANN : Ein von Herrn G. Oertel angeblich bei Dessau beobachteter *Carex*-Bastard.

Verhandlungen des Botanischen Vereins der Provinz Brandenburg (*continued*).

WARNSTORF: Die Acutifoliumgruppe der europäischen Torfmoose. Ein Beitrag zur Kenntniss der Sphagna (Taf. III und IV).

HENNINGS: Botanische Mittheilungen.

SCHINZ: Beiträge zur Kenntniss der Flora von Deutsch-Südwest-Afrika und der angrenzenden Gebiete, II und III.

WINKELMANN: Ein Ausflug nach Hinterpommern.

HUTH: Die Hakenklimmer.

———: Ueber stammfrüchtige Pflanzen.

KOEHNE: Eine neue *Cuphea* aus Argentinien.

TAUBERT: Ueber zwei aus dem märkischen Gebiet bisher nicht bekannte Gramineen, *Panicum ambiguum*, Guss., und *Melica picta*, C. Koch.

BEHRENDSEN: Ein Vorkommen von Adventivpflanzen zu Rüdersdorf bei Berlin.

WARNSTORF: Ein Ausflug nach der Uckermark.

HENNINGS: *Aecidium Schweinfurthii*, n. sp.

———————: Mycologische Excursionen.

MAGNUS: Anmerkung über Polysaccum in der Prov. Brandenburg.

TAUBERT: Beitrag zur Flora der Neumark u. des Oderthales.

BEYER: Ueber *Primula macrocalyx*, Bunge, u. *P. inflata*, Lehmann.

JACOBASCH: Mittheilungen.

Verhandlungen des Naturforschenden Vereins, Brünn. XXVI.

FORMANEK: Mährisch-Schlesische Menthen.

Verhandlungen des naturhistorischen Vereins der preussischen Rheinlande, Westfalens und des Reg.-Bezirks Osnabrück. Jahrgang XLV. Hälfte 1.

HERPELL: Präpariren und Einlegen der Hutpilze für das Herbarium.

Verhandlungen des Naturwissenschaftlichen Vereins in Karlsruhe. Bd. X (1883–1888).

SCHRÖDER: Veredelung von Pflanzen.

LEUTZ: Flora der Hochmoore von Kaltenbronn; die Wasserfarn bei Karlsruhe.

SCHWEICKERT: Die gefüllte Ranunkel bei Lautenbach.

GRÄBENER: Keimgerste in altem Wickellehm; die Ameisen in Gewächshäusern.

————: Reispflanze im Kiemen eines Goldfisches; Knospenvariation.

LYDTIN: Die Pasteur'sche Impfung gegen Hundswuth.

REBMANN: Umbildung von Fuchsienblüthen.

LEUTZ: Seltene Pflanzen bei Walldorf u. Waghäusel.

SCHUBERG: Die Schaftformen der Waldbäume.

Zeitschrift für Naturwissenschaften Halle.

Folge 4, Band VII.

Heft 5. OVERBECK: Bacteriologische Versuche um die Fähigkeit der Magnesia, Spaltpilze zu tödten, festzustellen.

„ 6. Ueber eine eigenthümliche Art der Verbreitung des *Chrysanthemum suaveolens* (Pursh.) Aschs.

Zeitschrift für wissenschaftliche Mikroskopie (Behrens).
Bd. V. Heft 4.

KLEIN: Beiträge zur Technik mikroskopischer Dauerpräparate von Süsswasseralgen, II.

ZSCHOKKE: Ueber einige neue Farbstoffe bezüglich ihrer Anwendung zu histologischen Zwecken.

NEUHAUSS: Verschiedenes über Mikrophotographie.

Bd. VI. Heft 1.

CAPRANICA: Sur quelques procédés de microphotographie.

Zeitschrift, Jenaische, für Naturwissenschaft.
Bd. XXIII (Neue Folge, Bd. XVI), Heft 2 und 3.

LIEBSCHER: Die Erscheinungen der Vererbung bei einem Kreuzungsprodukte zweier Varietäten von *Hordeum sativum*.

HILDEBRAND: Ueber einige Pflanzenbastardierungen (Taf. XXV und XXVI).

Zeitung, Botanische. Jahrg. XLVII.

No. 1. WIESNER: Der absteigende Wasserstrom u. dessen physiologische Bedeutung (continued in No. 2).

„ 2. MOLISCH: Ueber den Farbenwechsel anthokyanhältiger Blätter bei rasch eintretendem Tode.

„ 4. ZOPF: Ueber Pilzfarbstoffe (continued in Nos. 5 and 6).

„ — ZUKAL: *Hymenoconidium petasatum*.

„ 7. REINKE: Ein Fragment aus der Naturgeschichte der Tilopterideen (continued in Nos. 8 and 9).

„ 9. WEHMER: Das Verhalten des oxalsauren Kalkes in den Blättern von *Symphoricarpus*, *Alnus* u. *Crataegus* (continued in No. 10).

„ 11. SORAUER: Mittheilungen aus dem Gebiete der Phytopathologie.

„ 12. WENT: Die Vacuolen in den Fortpflanzungszell der Algen.

„ 13. Ueber die Schwankungen der Aufblühzeit.

„ 14. WORTMANN: Beiträge zur Physiologie des Wachsthums (continued in Nos. 15–18).

„ 19. DE VRIES: Ueber die Permeabilität der Protoplaste für Harnstoff (continued in No. 20).

„ 21. MEYER: Ueber die Entstehung der Scheidewände in dem sekretführenden, plasmafreien Intercellularraume der Vittae der Umbelliferen (continued in Nos. 22 and 23).

„ 24. NOACK: Ueber mykorhizenbildende Pilze.

GREAT BRITAIN.

Album, The Orchid.

Vol. VIII contains plates of—*Saccolabium coeleste*, Rchb. f.; *Cattleya Massaiana*; *Burlingtonia fragrans*, Lindl.; *Miltonia spectabilis Moreliana*, Henfrey; *Cypripedium Williamsianum*, Rchb. f.; *Odontoglossum Harryanum*, Rchb. f.; *Ansellia Africana*, Lindl.; *Oncidium undulatum*, Lindl.; *Cirrhopetalum ornatissimum*, Rchb. f.; *Cypripedium cardinale*, Rchb. f.; *Laelia Gouldiana*, Rchb. f.; *Laelia majalis*, Lindl.; *Oncidium splendidum*, A. Rich.; *Aganisia coerulea*, Rchb. f.; *Lycaste cruenta*, Lindl.; *Odontoglossum Oërstedii*, Rchb. f.; *Majus*, n. var.; *Eriopsis rutidobulbon*, Hook.; *Calanthe biloba*, Lindl.; *Cypripedium oenanthum*, Rchb. f.; *C. Wallisii*, Hort.

Annals of Botany.

Vol. II (*continued*).

No. VIII. Botanical Necrology for 1888.

Record of Current Literature, 1888 (*continued*).

Vol. III.

No. IX. MIYABE: On the life-history of *Macrosporium parasiticum*, Thüm. (Pl. I and II).

LOWE AND JONES: Abnormal Ferns, Hybrids, and their Parents (Pl. III).

COOKE AND MASSEE: A new Development of *Ephelis* (Pl. IV).

BARBER: On the Structure and Development of the Bulb in *Laminaria bulbosa*, Lamour (Pl. V and VI).

SCHUNCK: On the Chemistry of Chlorophyll (Pl. VII).

TURNBULL: Preliminary note on the Distribution and Structure of Water-pores on Cotyledons (Woodcuts 1–5).

LOWE: A Discovery in connection with the production of Hybrid Ferns.

MURRAY AND BOODLE: Further note on *Spongocladia*.

FARMER: Preliminary note on the Morphology and Development of *Isoëtes lacustris*.

OLIVER: On a new form of *Trapella sinensis*.

Annual Report of the Wellington College Natural Science Society. XIX.

Phenological report.

Bulletin of Miscellaneous Information. Royal Gardens, Kew, 1889. LXXVI–CIII.

No. 25. Coca.
,, — Beetles destructive to rice-crops in Burma.
,, — Fibre from Lagos.
,, — Yam-Bean.
,, — Schweinfurth's Method for Preserving Plants.
,, — A starch-yielding Bromeliad.
,, — The Fruits of Mysore.
,, 26. Seeds of Herbaceous Plants.
,, 27. Fibre industry at the Bahamas.
,, — Hardy species of *Eucalyptus*.
,, — Yam-Bean.
,, — West African rubbers.
,, — Phylloxera in Asia Minor.
,, — Botanical station at Lagos.
,, — Chiga bread.
,, 28. New Garden Plants.
,, 29. Persian Zalil.
,, — Tasmanian Woods.
,, — Lily flowers and bulbs used as food.
,, — P'u-êrh tea.
,, — Short-podded Yam-Bean.
,, 30. Jamaica cogwood.
,, — Cocoa-nut Coir from Lagos.
,, — A wheat pest in Cyprus.
,, — Patchouli.
,, — P'u-êrh tea.
,, — Agricultural industries at the Gambia.

Chemical News, The. Vol. LIX.

No. 1519. MACADAM: On some new fossil resins from the coal measures.
„ 1523. RAWSON: On some new tests for Tannic and Gallic acids.
„ 1530. CROSS AND BEVAN: The Chemistry of the Flax Fibre.
„ 1535. LANDRIN: On the Analysis of Cinchonas.
„ 1539. WHITE: Indigo Stem Ash.
„ 1540. ———: Estimation of Tea Tannin.
„ — PALMER: The testing of Logwood extracts.

Gazette, Agricultural Student's. Vol. IV, Part 2.

GILBERT: Results of experiments at Rothamsted on the growth of Potatoes.

Chronicle, The Gardeners'. Series 3. Vol. V.

No. 106. Novelties of 1888 (continued in No. 107).
„ — REICHENBACH, F.: *Peristeria Rossiana*, n. sp.; *Cypripedium Crossianum* × *Psittacinum*, n. hyb., Angl.
„ — O'BRIEN: Culture of S. African Orchids.
„ — MASTERS: Monstrous Ivy flowers.
„ — Cultivation of useful plants in Hainan (concluded from Vol. IV).
„ 107. Chrysanthemum sports.
„ — ROLFE: *Cypripedium margaritaceum*, Franch.
„ — REICHENBACH, F.: *Cypripedium insigne Horsmanianum*, Rchb. f.; *Cypripedium Crossianum Tautzianum* × Rchb. f.; *Epidendrum radiatum* (Lindl.) *fuscatum*, n. var.
„ — *Tachiadenus carinatus.*
„ — *Pinus Sabiniana* at Kew (Fig. 6).
„ — Roots of Leguminosae.
„ — Genera of Ferns.
„ 108. REICHENBACH, F.: *Cypripedium Pitcherianum*, n. hyb., Angl. (Fig. 10); *Schomburgkia Lepidissima*, n. sp.; *Castasetum galeritum* (Rchb. f.) *pachyglossum*, n. var.
„ — MORRIS: *Agave candelabrum* (Fig. 11).
„ — ROLFE: *Phalaenopsis amabilis.*
„ 109. REICHENBACH, F.: *Laelia anceps* (Lindl.), var. *amabilis*, n. var.
„ — Useful Ferns.
„ — *Cattleya Loddigesii* (Fig. 13).
„ — BURBIDGE: Flower colour.
„ — The Chinese Primrose (continued in No. 110).
„ 110. *Ixianthes retzioides* (Fig. 19).
„ — BROWN: *Arisaema Wrayi*, Hemsley; *Satyrium membranaceum*, Swartz.
„ — ROSS: The Australian Pitcher Plant.
„ — A turnip gone wrong (Fig. 21 and 22).
„ 111. REICHENBACH, F.: *Cypripedium insigne Hallianum*, n. var.; *Cypripedium claptonense* × n. hyb., Angl.
„ — *Castasetum fimbriatum* (Lindl.) *platypterum*, n. var.
„ — BROWN: *Habenaria Macowaniana*, n. sp.
„ — MASTERS: *Abies lasiocarpa*, Hooker (Figs. 23–32).
„ — Tenacity of Life in a Cycad.
„ — BURBIDGE: Plant colour.

Chronicle, The Gardeners' (*continued*).

„ 112. ROLFE: *Cypripedium Cassiope* × n. hyb.; *Eria marginata*, n. sp.
„ — REICHENBACH, F.: *Masdevallia Courtauldiana* × n. hyb., Angl.
„ — A new Australian fruit, *Kunzea pomifera* (Fig. 36).
„ — The Japan Lacquer Tree (*Rhus vernicifera*).
„ 113. Seeds and the season.
„ — REICHENBACH, F.: *Odontoglossum luteo-purpureum* (Lindl.), var. *crispatum*. n. var.; *Vanda Kimballiana*, n. sp.; *Vanda Amesiana*, Rchb. f.; *Saccolabium giganteum illustre*, Rchb. f.
„ — BAKER: *Gladiolus Adlami*, n. sp.
„ — MARSHALL WARD: Smut-fungi (continued in No. 114).
„ — *Abies bracteata*, Nuttall (Fig. 44).
„ 114. P. E. N.: A history of English gardening (continued in Nos. 116 and 126).
„ — REICHENBACH, F.: *Cattleya Ballantiniana* × n. hyb.; *Dendrobium Harveyanum*, Rchb. f.
„ — SMITH: Disease of Snowdrops.
„ 115. BUNYARD: Modern fruit-culture (Figs. 50–54).
„ — ROLFE: *Dendrobium chrysodiscus* × and *D. melanodiscus* × *Bulbophyllum suavissimum*, n. sp.
„ — F. R.: Cycads and their culture.
„ — *Barnardesia rosea* (Fig. 55).
„ 116. D. D.: Saxifrages (Figs. 60–64).
„ — BAKER: *Iris* (sect. *Onocyclus*) *atropurpurea*, n. sp.
„ — DAMMER: Double flowers caused by mites.
„ 117. BROWN: *Disa tripetaloides*, N. E. Br.
„ — MASTERS: *Pinus Jeffreyi*, Balfour (Figs. 65, 68).
„ — SMITH: Fungus on cucumber plants, *Didymium Daedaleum*, B. and Br. (Fig. 66).
„ — Saxifrages (Fig. 67).
„ — HANS: *Abies Eichleri*.
„ 118. REICHENBACH, F.: *Cypripedium* × *robustius* × *sedeni* = *longifolium*, n. hyb., Vindob.
„ — ROLFE: *Castasetum Darwinianum*, n. sp.
„ — O'BRIEN: *Cypripedium venusto-Spicerianum* × *Shortia galacifolia*.
„ 119. The Camellia (Figs. 76–78).
„ — ROLFE: *Cypripedium T. B. Haywood*, n. hyb.
„ — REICHENBACH, F.: *Odontoglossum Harryanum pavonium*, n. var., *Eucalyptus Staigeriana* (Fig. 81).
„ 120. BAKER: *Galanthus Fosteri*, n sp.
„ — ROLFE: *Xylobium leontoglossum*, *X. corrugatum*.
„ — R. A. R.: *Odontoglossum nebulosum*, var. *candidulum*, Rchb. f.
„ — DOD: The daffodil rot.
„ — BROWN: Sexuality in *Catasetum* (Fig. 83).
„ — WARD: Chlorosis.
„ 121. REICHENBACH, F.: *Dendrobium chlorostele* × *xanthocentrum*, n. hyb.
„ — ROLFE: *Odontoglossum crispum*, Stevens' var.
„ — *Dendrobium Wardiano* × *aureum*, n. hyb.
„ — ROLFE: List of Garden Orchids (continued from new series, Vol. XX), (continued in Nos. 123, 125, 126, 128, 129, 131).
„ — *Mutisia clematis* (Fig. 88).

Chronicle, The Gardeners' (*continued*).
,, — F. V. M.: Tenacity of Life in Seeds of *Poinciana Regia*.
,, 122. MASTERS: Skimmias (Figs. 89–91) (continued in No. 123).
,, — BROWN: *Bambusa tesellata*, Munro; and *B. Veitchii*, Carrière.
,, — SHELFORD: *Iris Rosenbachiana*.
,, 123. ROLFE: *Selenipedium Isabelianum*, Rodr.
,, — REICHENBACH, F.: *Angraecum polystachys*, P. Th.; *A. Kimballianum*, Hort. Seeg., and Tropp.
,, — LYNCH: *Aphelandra cristata*.
,, — *Anoiganthus breviflorus* (Fig. 95).
,, — The Philosophy of the Auricula.
,, 124. D. R. P.: Fruit culture in 1757.
,, — GUMBLETON: *Sphaeralcea nutans*, Schweidler.
,, — ROLFE: *Oncidium fimbriatum*, Lindl.; *Pholidota ventricosa*, Rchb. f.
,, — FOSTER: *Iris Caucasica* and *I. Orchioides*.
,, — CORREVON: A few Alpine Crucifers (concluded from Vol. IV).
,, — HEMSLEY: The Chinese and Japanese species of *Buddleia*.
,, — F. R.: The Àmancaes.
,, 125. ROLFE: *Masdevallia Chelsoni splendens*, Veitch.
,, — Laurels and Laurels (Figs. 105–106).
,, — PAUL: Vitality of Seeds.
,, — WEATHERS: *Cypripedium Curtisi* (Fig. 108).
,, 126. BAKER: *Muscari Maweanum*.
,, — ROLFE: *Odontoglossum excellens* × Rchb. f.—a natural hybrid.
,, — *Lathraea clandestina* (Fig. 110).
,, — DOD: *Ranunculus*.
,, 127. *Masdevallia Parlatoreana* × Rchb. f.
,, — Californian Forestry.
,, — ROLFE: *Laelia grandis*, Lindl., *Dendrobium crassinode* × *Wardianum*.
,, — SIMMONDS: The economic use of barks.
,, — THOMPSON: Vegetation after forest fires.
,, 128. BENNET, H.: Vegetation on the Lime soils of the Mediterranean.
,, — ROLFE: *Masdevallia caudata* × *Estradae*, n. hyb.
,, — *Aesculus Sinensis*, Bunge (Fig. 116).
,, — SMITH: Disease of Daffodils: *Puccinia Schroeteri*, Pass.
,, — BONAVIA: *Iris Iberica*.
,, 129. ROLFE: *Laelio-Cattleya* × *Dighyana-Mossiae*, n. hyb.
,, — *Masdevallia Parlatoreana* × Rchb. f.
,, — A Vegetable Titan.—*Amorphophallus Titanum*.
,, 130. ROLFE: *Epidendrum Campylostalix*, Rchb. f. (Illustrated.)
,, — ———: *Dendrobium chrysolabrum*, n. sp.
,, — Male flowers of *Saxe-gothea* (Fig. 125).
,, 131. ROLFE: *Dendrobium Fairfaxii*, n. sp.
,, — ———: *Zygopetalum* (*Huntleya*) *lucidum*, n. sp.
,, — SMITH: Disease of Lilies.—*Polyactis cana*, B.
,, — *Torreya californica*, Torr.; male and female flowers (Figs. 126, 127).
Gossip, Science. 1889.
No. 289. PORTER: White varieties of plants.
,, — STYAN: A good hunting-ground for Orchids in Kent.

Gossip, Science (*continued*).

„ 290. TANSLEY: Colour development in Leaves and Flowers (continued in No. 291).
„ 291. COUPAR: Abnormal growths on forest-trees.
„ — MALET: Notes on the Flora of the Wye.
„ 292. TAYLOR: Soils, their origin, etc.
„ — DARBISHIRE: Notes on *Oedogonium*.
„ — BODINGTON: The Flora of the past (continued in Nos. 293 and 294).
„ — COCKERELL: Colorado Fungi.
„ 293. ROBERTSON: The development of the colours of Flowers through Insect selection.
„ 294. DARBISHIRE: Organisms in chemical solutions.
„ — BULMAN: The Bee and the Willow.

Grevillea. Vol. XVII.

No. 83. COOKE: Synopsis Pyrenomycetum (continued in No. 84).
„ — ———: Australasian Fungi.
„ — ———: New British Fungi (continued in No. 84).
„ — ———: Some Exotic Fungi (continued in No. 84).
„ — ———: Some Brisbane Fungi.
„ — ———: Three Natal Fungi.
„ — MASSEE: British Pyrenomycetes (continued in No. 84).
„ — Diagnoses omitted from Saccardo's 'Sylloge.'
„ 84. MASSEE: On *Erysiphe polychaeta*, B. and C., and *Uncinula polychaeta*, B. and C.
„ — COOKE: Two Australian Fungi.
„ — ———: What is *Lichenopsis*?
„ — Thelephorei.

Icones Plantarum (Hooker's). Vol. IX.

Part I contains plates and descriptions of—*Phialanthus myrtilloides*, Griseb.; *Mimosa bahamensis*, Benth.; *Acacia acuifera*, Benth.: *A. choriophylla*, Benth.; *Salmea petrobioides*, Griseb.; *Buxus bahamensis*, Baker, n. sp.; *Pinus bahamensis*, Griseb.; *Liparis Cathcartii*, Hook, f.; *L. Glossula*, Rchb. f.; *L. pulchella*, Hook. f.; *L. cordifolia*, Hook. f.; *L. Gamblei*, Hook. f.; *L. rostrata*, Rchb. f.: *Sonerila peperomiaefolia*, Oliv., n. sp.; *Faberia sinensis*, n. gen. et sp.; *Rubus hupehensis*, Oliv., n. sp.; *Holboellia cuneata*, Oliv., n. sp.; *Cardamine paradoxa*, Hance; *Clematis Henryi*, Oliv. n. sp.; *Mesembryanthemum Barklyi*, N. E. Br. n. sp.; *Ranunculus macropetalus*, DC.; *Hemsleya chinensis*, Cogn. n. gen. et sp.; *Emmenopterys Henryi*, Oliv. n. gen. et sp.; *Ficus foveolata*, Wall. var. *Henryi*; *Stauro-chlamys Burchellii*, Bak. n. gen. et sp.

Part II contains plates and descriptions of—*Microstylis Maingayi*, Hook. f. n. sp.; *M. furcata*, Hook. f. n. sp.; *M. parvula*, n. sp.; *Ranunculus calandrinioides*, Oliv. n. sp.; *Ononis Thomsoni* Ball. Mss. n. sp.; *Microstylis lancifolia*, Thw.; *M. khasiana*, Hook. f.; *M. Rheedii*, Wight.; *M. Stocksii*, Hook. f.; *M. micrantha*, Hook. f. n. sp.; *M. acutangula*, Hook. f.; *Liparis Trimenii*, Ridl.; *Inocarpus edulis*, Forst.; *Tryphostemma triloba*, Bolus, n. sp.; *Osteospermum tanacetifolium*, Macowan; *Ceratandra Harveyana*, Lindl.; *Disa Charpentieriana*, Rchb. f.; *Pachyrrhizus angulatus*, Rich.; *P. tuberosus*, Spreng.;

Icones Plantarum (*continued*).

Chisocheton princeps, Hemsl. n. sp.; *Eria alba*, Lindl.; *E. excavata*, Lindl.; *E. graminifolia*, Lindl.; *E. alata*, Hook. f. n. sp.; *E. acervata*, Lindl.; *E. confusa*, Hook. f. n. sp.

Part III contains plates and descriptions of—*Aechmea Skinneri*, Baker; *Gastrodia orobanchoides*, Benth.; *Dendrobium nanum*, Hook. f. n. sp.; *Liparis macrantha*, Hook. f.; *L. lancifolia*, Hook. f.; *L. pusilla*, Ridl.; *L. perpusilla*, *L. Prainii*, Hook. f.; *L. Duthisi*, Hook. f.; *L. bistriata*, Par. et Rchb. f.; *Dendrochilum linearifolium*, Hook. f.; *Tainia macrantha*, Hook. f. n. sp.; *T. cordifolia*, Hook. f. n. sp.; *Zizyphus Chloroxylon*, Oliv.; *Ilex racemosa*, Oliv. n. sp.; *Calanthe phajoides*, Rchb. f.; *Diphylax urceolata*, Hook. f. n. gen. et sp.; *Isachne comata*, Munro; *Tupistra chinensis*, Baker, n. sp.; *Dioscorea rhipogonoides*, Oliv. n. sp.; *Andropogon exaltatus*, R. Br.; *A. ceresiaeformis*, Nees; *A. laniger*, Desf.; *Microtoena cymosa*, Prain, n. gen. et sp.; *Gymnotheca chinensis*, Dene; *Gmelina chinensis*, Benth.; *Pinellia integrifolia*, N. E. Br. n. sp.

Journal and Transactions, The Pharmaceutical. Series 3.

No. 967. Hooper: Laurel-Nut Oil.
„ 969. Chemical notes on Coca.
„ — Cinchona cultivation in Columbia.
„ — Coca and Cocaine.
„ 970. Dymock and Hooper: *Podophyllum Emodi*.
„ — Hirschsohn: Detection of Cotton-Seed Oil in Olive Oil.
„ — Cacao cultivation in Colombo.
„ 971. Alkaloids of the Areca Nut.
„ — Strophanthus and Strophanthin.
„ — Asparagin and Tyrosin in the Dahlia.
„ — *Magnolia glauca*.
„ 972. Duncan: Extract of *Nux Vomica*.
„ — Hill: The American *Tinctura Quillajae*.
„ 973. Moss: Note on *Cascara Sagrada*.
„ 974. The Alkaloids of the Areca Nut and the physiological action of Arecoline.
„ 975. *Bacterium coli* and *B. lactis*.
„ — *Eschscholtzia californica*.
„ — Condurango bark.
„ — *Acacia anthelmintica*.
„ — *Senecio canicida*.
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„ 977. Martindale: Note on Egyptian Opium and some other drugs.
„ — *Cascara Sagrada*.
„ 978. Holmes: Further notes on Massoi Bark.
„ — Hurst: Note on Gamboge.
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„ — Thomson: Note on the Green Euonymin.
„ 979. Oil of Myrtle and Myrtol.
„ — Hydrangin.
„ — The Sugar of Fungi.
„ — China Morada.
„ — *Polypodium Friederichsthalianum*.

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„ 981. Oil of Bay Leaves.
„ 982. Fixing of the Spores of Hymenomycetes.
„ — Notes on Essential Oils.
„ 983. Constitution of Cinchona Alkaloids.
„ — HESSE: Chemistry of the Coca bases.
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„ 987. GREENAWALT: Oleoresin of Male Fern.
„ 989. Jamaica Sarsaparilla.
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„ — FRYER: Notes on Pond-weeds (continued in Nos. 314 and 315).
„ — MCARDLE: Hepaticae of Wicklow.
„ — MOYLE ROGERS: Notes on the Flora of South Hants.
„ — BRITTEN AND BOULGER: Biographical Index of British and Irish Botanists (continued in Nos. 314–318).
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„ — NICHOLSON: Extracts from Report of the Botanical Exchange Club for 1887.
„ 315. MURRAY, G. AND BOODLE: A Systematic and Structural account of the Genus *Avrainvillea*, Decne (continued in No. 316).
„ — BEDDOME: Two new Athyriums from the N. W. Himalayas.
„ — HANBURY: Further Notes on *Hieracia* new to Britain.
„ — BUCHANAN WHITE: The Collecting and Study of Willows.
„ — FRYER: *Gnaphalium uliginosum*, L., var. *pilulare*, Wahl.
„ — SCULLY: Further notes on the Kerry Flora.
„ 316. BRITTEN: Dr. Seemann's Study-set.
„ — MOFFAT: Plants near Ballyhyland, Co. Wexford.

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„ 316. HANBURY AND MELVILL: New County Records for Sutherland, Caithness, and Ross.
„ — H. AND J. GROVES: On *Epilobium alpinum* and *E. anagallidifolium*.
„ — New Phanerogams published in Periodicals in Britain during 1888 (continued in No. 317).
„ 317. MASTERS: *Abies lasiocarpa*, Hook., and its allies.
„ — KIRK: A new Chenopodium from New Zealand.
„ — TOWNSEND: *Ranunculus Steveni*, Andrz. and *R. acris*, L.
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,, 9. MACLEOD AND MILLES: An inquiry into the Causation of Asiatic cholera (continued in No. 10).
,, 10. The Cholera Bacillus.
,, 11. Cultivation of Cinchona in Bengal.

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Nos. 529–534 contain plates and descriptions of:—*Brownea macrophylla*, Masters; *Olearia insignis*, Hook. f.; *Rosa incarnata*, Mill.; *Streptocarpus parviflora*, E. Meyer; *Macodes Iavanica*; *Strelitzia Nicolai*, Regel; *Styrax Obassia*, Sieb. and Zucc.; *Iris Meda*, Stapf.; *Opuntia Rafinesquii*, Engelm.; *Dendrobium gracilicaule*, F. Müll.; *Eremostachys laciniata*, Bunge; *Delphinium Zalil*, Aitchison et Hemsley; *Iris Barnumae*, Foster et Baker; *Calandrinia oppositifolia*, S. Wats; *Passiflora Hahnii*, Masters; *Lilium nepalense*, D. Don; *Sarcochilus luniferus*, Benth. mss.; *Stuartia Pseudo-camellia*, Max.; *Opuntia polyacantha*, Haworth; *Chironia peduncularis*, Lindl.; *Licuala Veitchii*, Wats.; *Smilax ornata*, Lemaire; *Pentstemon rotundifolius*, A. Gray; *Saxifraga latepetiolata*, Wilkomm et Lange; *Laportea maroides*, Wedd.; *Sobralia leucoxantha*, Rchb. f.; *Enkianthus campanulatus*; *Spathoglottis ixioides*, Lindl.; *Angraecum Germinyanum*, Hort.; *Solanum pensile*, Sentdn.

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,, 163. ADDISON: *Agaricus* (*Pleurotus*) *revolutus* near Thirsk.
,, 164. BENNETT: *Geranium macrorhizum* and *Carex gibsoni* in West Yorkshire.
,, — WEST: Additions to the Algae of West Yorkshire (continued in No. 165).
,, — *Physcomitrella patens* in Derbyshire.
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,, 135. MATHEWS: History of the county Botany of Worcester (continued from Vol. XI and further continued in No. 136).
,, 138. GROVE AND BAGNALL: The Fungi of Warwickshire.

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„ — BEEBY: On the Flora of Shetland.
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„ — DRUCE: Plants of Peebleshire.
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„ 1005. MORRIS: A Jamaica Drift-Fruit.
„ 1008. The School of Forestry at Dehra Doon, India.
„ 1013. WARD: Beech-wood.
„ 1016. Afforestation in China.
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„ 9. Caruel: Contribuzione alla flora delle Galapagos.

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———: Sul fungo che è causa del Bitter-Rot degli Americani.

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,, — ———: Sulla struttura dei semi della *Nymphaea alba.*
„ — DE TONI: Prima contribuzione diatomologica sul lago di Alleghe.
,, — CARUEL: Conspectus familiarum phanerogamarum.
„ — ARCANGELI: Sulla struttura del seme del *Nuphar lutea*, Sm.
,, — CUBONI: Sulla erinosi nei grappoli della Vite.
„ — TERRACCIANO: Le piante spontanee dell' Isola Minore nel lago Trasimeno.
,, — PIROTTA: Sui pronubi dell' *Amorphophallus Rivieri*, Dur.
„ — CUBONI: Sulla cosidetta uva infavata dei colli Laziali.
,, 2. MACCHIATI: La *Synedra pulchella*, Kütz., var. *abnormis*, M., et altre Diatomacee della sorgente di Ponte Nuovo.
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„ — CICIONI: Sopra una varietà della *Myosotis intermedia*, e del *Polygonum dumetorum.*
„ — GOVIAN: Alcune notizie sulla flora veronese.
„ — ARCANGELI: Sulla funzione trofilegica delle foglie.
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„ — MARTELLI: Una nuova specie di Riccia.
„ — ———: Sul *Polyporus gelsorum*, Fr.
„ — CELOTTI: Contribuzione alla micologia romana.
„ — AVETTA: Contribuzione alla flora dello Scioa.
„ — PIROTTA: Osservazioni sopra alcuni Funghi.
„ — LUMIA: Del miscuglio gassoso nel sicono del Fico (*Ficus Carica*).
„ — TERRACCIANO: Le Viole italiane spettanti alla sezione *Melanium*, DC.
„ — CUBONI: Esperienze per la diffusione della *Entomophthora grylli*, Fres., contro le cavallette.

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„ — Campani e Grimaldi: Contribuzione alle conoscenze chimiche nei semi del lupino bianco.
„ 9. Piutti: Sintesi e costituzione delle asparagine.
„ 10. De Blasi: La tifotoxina del Brieger.
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Fasc. 3. Funaro: Intorno alla Senegina, glucoside della *Polygala virginiana*.
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„ — Genmari: Florula di Palabanda.
„ — Mueller: Lichenes Spegazziniani in Staten Island, Fuegia et in regione freti Magellanici lecti.
„ — De Toni: Note sulla flora del Bellunese.
„ — Mori: Enumerazione dei Funghi delle provincie di Modena e di Reggio (*continued*).
„ — Nicotra: Elementi statistici della flora siciliana (*contin.*).
„ 2. Massalongo: Nuovi Miceti dell' agro veronese.
„ — Piccone: Alghe della crociera del Corsaro alle Azzorre.
„ — Ross: Contribuzioni alla conoscenza del tessuto assimilatore e del o sviluppo del periderma nei fusti delle piante povere di foglie o afille.
„ — Micheletti: Index schedularum criticarum in Lichenes exsiccatas Italiae.
„ — Martelli: Caso teratologico nella *Magnolia anonaefolia*, Salisb.

Malpighia. Anno III.

Fasc. I, II.

Arcangeli: Sopra l'esperimento di Kraus.
De Toni: *Boodlea*. Murr. et De Toni, nuovo genere di Alghe a fronde reticolata.
Acqua: Nuova contribuzione allo studio dei cristalli d'ossalato di calcio nelle piante (Tav. I).
Berlese: Rivista delle Laboulbeniacee e descrizione d'una nuova specie di questa famiglia (Tav. II).
Pirotta: Intorno all' amido della epidermide di certi Rhamnus.
De Toni: Sopra due Alghe Sud-Americane.
Fayod: Sopra un nuovo genere di Imenomiceti (con incisioni nel testo).
Brizi: Muschi nuovi per la provincia di Roma.
Penzig: Piante nuove o rare trovate in Liguria.

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Fasc. II, III.

DELPINO : Valore morfologico della squama ovulifera delle Abietinee e di altre Conifere.

BOTTINI : Noterelle briologiche (con Tav. III–V).

FAYOD : Note sur une nouvelle application de la photographie en botanique (Tav. VI).

MARCATILI : Sui fasci midollari fogliari dei Ficus.

BELLI : Osservazioni su alcune specie del gen. *Hieracium*, nuove per la Flora pedemontana.

———: Le Festuche italiane del R. Museo Botanico Torine e.

MATTIROLO E BUSCALIONI : Sulla struttura degli spazii intercellulari nei tegumenti seminali delle Papilionacee (con Tav. VII).

ACQUA : Alcune osservazioni sul luogo d'origine dell' ossalato calcico nelle piante (con incisione nel testo).

BRIZA : Prima contribuzione all' Epatologia romana.

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STEFANI : Sopra una galla di Phytopitus sul *Vitex agnus-castus*.

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N. 13. DE TONI : *Pilinia*, Kuetz. ed *Acroblaste*, Reinsch.

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„ — RACIBORSKI : Su alcune Desmidiacee lituane.

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„ — Algae novae, diagnoses.

N. 14. LEWIN : Ueber spanische Süsswasseralgen.

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BARBAGLIA : Sull' olio essenziale di *Laurus nobilis*.

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GASPERINI : De fermentazioni e le proprietà del Leghbi o vino di palma, con notizie del Prof. Spigai sulla estrazione e sugli usi.

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Vol. II, Fasc. 12.

ALBINI : Osservazioni sui vegetali segregati.

Vol. III, Fascic. 4.

GASPARIS : Sul pulviscolo atmosferico.

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COCCONI : Contributo allo studio dei nettarii mesagamici delle Caprifogliacee.

DELPINO : Applicazione di nuovo criteri per la classificazione delle piante.

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Rendiconto delle Sessioni della R. Accademia della Scienze dell' Instituto di Bologna (*continued*).

TRIZZONI E MIRCOLI: Della infezione setticoemica specialmente di quella determinata dallo Streptococco piogeno.

BELLONCI: Sulla divisione diretta del nucleo.

MORINI: Biografia degli apoteci della *Lachnea theleboloides* (A. et S.), Sacc.

———: Contribuzione all' anatomia microscopica dell' embrione delle Cupilifere.

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BALAKCHINE ET VANIUKOFF: Culture de la pomme de terre.

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Korresp. Blatt des Naturforscher-Verein, Riga. XXXI.

WESTBERG: Hoftüpfel.

Kosmos We Lwowie. Rok XIV. Zeszyt I–III.

REHMANA: Naegelego i Petera monografia Jastrzębców (*Hieracium*) i znaczenie tego dziela dla systematyki roślin w ogólności (continued in Zeszyt IV–V).

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HISINGER: Tubercules du *Ruppia*, Rostell. et du *Zanichellia Polycarpa*, provoqués par le Tetramyxa Parasit.

LINDBERG: Nordes Mossflora.

KARSTEN: Symbolae ad Mycologicam fennicam.

KIHLMANN: *Potamogeton vaginatus*, Turcz.

BRENNER: *Festuca duriuscula*, L. i Finland.

SAELAN: *Eritrichium villosum* (Ledeb.), Bunge.

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„ — GORDJAGIN : Flora der Umgebungen von Krasnoufimsk im Gouv. Perm.

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No. 5. WOTHTSCHALL : Zur Frage von der Verbreitung, Vertheilung und Rolle des Solanin's in den Pflanzen. II. Das Geschick des Solanin's in der Pflanze und seine Bedeutung für das Leben derselben

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THEDENIUS: Om *Potentilla thuringiaca*, Bernh. i Sverige.

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ALMQUIST: Om en egendomlig form af *Potamogeton filiformis*.

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————: Om gruppindelning och hybrider inom slägtet Potamogeton.

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„ 342. Bubach (an insecticide prepared from flowers of *Pyrethrum cinerariæfolium*).

„ 345. Olive Cultivation.

Report of State Board of Agriculture. Kansas (*continued*).

No. 347. Plant-life of Arabia Felix.
„ 354. Atmospheric nitrogen as plant-food.
„ —— The Ethnological significance of the beech.
„ 355. Protoplasm and its history.

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No. 42. COCKERELL: Notes on the Flora of Custer County, Colorado, III.
„ 43. The Desert (Colorado) in June (Vegetation of).
„ — PALMER: Changes in the color of grapes grown in N. W. Mexico.
„ — ORCUTT: *Cereus Cochal,* n. sp.
„ — ———: Some native forage plants of S. California (continued in No. 44).
„ 44. The Loco Weed.
„ 45. Contributions to N. American Botany, I. *Hosackia Haydoni*, n. sp. *Hookera Orcuttii*, Greene.
„ — ORCUTT: Trees and Shrubs of San Diego County, California.
„ — PALMER: Opuntia fruit as an article of food.
„ — Albinism among flowers.
„ 46. On the medical properties of some California plants.
„ — LOPATECKI: The trees of British Columbia.
„ 47. PARRY: *Eriogonum fastigiatum*, n. sp.
„ 48. ORCUTT: Flora of the Alamo.
„ — COCKERELL: Flora of Wet Mountain Valley, Colorado. Monocotyledons (continued in No. 49).
„ — ORCUTT: Contributions to N. American Botany, II. *Pholisma arenarium*, Nutt., *Ammobroma sonorae*, Torr.
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No. 1. NAIRNE: An address to students of botany in W. India.
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,, 2. LISBOA, MRS. J. C.: Short notes on the odoriferous grasses (Andropogons) of India and Ceylon, with description of a supposed new species. (Plate.)
,, — Parasitic trees.

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———: On air-gas for bacteriological work.

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„ 6. ———— : *Chloanthes Teckiana*, n. sp. from West Australia.
„ 7. TISDALL : Fungi of the season.
„ — MÜLLER : *Logania chorebroides*, n. sp.
„ 8. ———— : *Prasophyllum Frenchii*, new for Victoria.

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„ 9. KRASSER: Versteinerter Wald bei Kairo.

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„ — BORBÁS: Die im Lemberger Universitätsherbarium aufbewahrten siebenbürgischen Nelkenarten.

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„ —— OTTO: A puoztai talpas-tyuk és a madárvonulas.
„ 235. BÉLA: Szövetkezes a novenyek között.
„ 236. LAJOS: Allatok es novenyek egymassal tarsulasa.
„ —— BÉLA: Tapasztalatok a novenyhonositas teren.
„ 237. SANDOR: A mezorendorsegi torvenyjavaslat.
„ 240. KAROLY: A hevvizi tunderrozsa budai termohelye.
„ 242. JÁNOS: A bambusz.
„ —— VINCZE: A nép botanikai legendajabol.
„ 243. A termesek es á a magvak (17 kepp.).

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III. Quartal.

BÜRGERSTEIN: Materialien zu einer Monographie, betreff. die Erscheinungen der Transpiration der Pflanzen, II.

FRITSCH: Ueber ein neues hybrides *Verbascum*.

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STRASSER: Zur Flechtenflora Niederösterreichs.

WIEMANN: *Saxifraga Braunii*, n. hyb.

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„ — WETTSTEIN: Die Gattungen *Erysimum* u. *Cheiranthus* (Pl. 1), (continued in Nos. 8, 9).
„ — CELAKOVSKÝ: Ueber *Potentilla Lindackeri*, Tausch, u. *P. radiata*, Lehm.

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No. 7. Ascherson: Zur Synonymie der *Eurotia ceratoides*, (L.) C. A. Mey. und einiger ägyptischer Paronychieen (continued in Nos. 8, 9).
„ — Dietel: Ueber die Aecidien von *Melampsora Euphorbiae dulcis*, Otth., u. *Puccinia silvatica*, Schröt.
„ — Lippitsch: Ueber das Einreissen der Laubblätter der Musaceen u. einiger verwandter Pflanzen.
„ — Celakovský: *Thymus quinquecostatus*, n. sp.
„ — Vandas: Beiträge zur Kenntniss der Flora von Süd-Hercegovina (continued in No. 8).
„ 8. Celakovský: *Althaea armeniaca*, Ten., in Ungarn.
„ — Zahlbrückner: Eine bisher unbeschriebene Sapotacee Neu-Caledoniens.
„ — Bäumler: Mycologische Notizen, II.
„ — Woloszczak: Kritische Bemerkungen über siebenbürgische Weiden (continued in No. 9).
„ 9. Willkomm: Neue Arten der spanisch-portugiesischen Flora.
„ — Wettstein und Sennholz: Zwei neue hybride Orchideen.
„ — Velenovský: *Lepidotrichum*, eine neue Cruciferen-Gattung.
„ — Sennholz: *Adenostyles canescens* (*glabra* × *Alliariae*).
„ — Bornmüller: Beitrag zur Flora Dalmatiens.
„ 10. Zukal: Ueber die Entstehung einiger Nostoc- u. Glœocapsa-Formen (continued in Nos. 11 and 12).
„ — Freyn: Plantae Kaosanae (continued in Nos. 11 and 12).
„ — Borbas: Ueber Arten der Gattung *Tilia* mit sitzenden Bracteen.
„ — Magnus: Kurze Notiz über bemerkenswerthe Vegetationserscheinungen im Sommer 1889.
„ — Krasan: Kalk u. Dolomit in ihrem Einflusse auf die Vegetation (continued in No. 11).
„ 11. Wettstein: Studien über die Gattungen *Cephalanthera*, *Epipactis*, u. *Limodorum* (Taf. 3), (continued in No. 12).
„ — Sabransky: Ein Beitrag zur Kenntniss der mährischen Brombeerenflora (continued in No. 12).
„ — Schilbersky: Beiträge zur Moosflora des Pester Comitates.
„ 12. Charrel: *Colchicum micranthum*, Boiss.
„ — Knapp: Die Heimat der *Syringa persica*, L.
„ — Braun: Ueber einige kritische Pflanzen der Flora von Nieder-Oesterreich.

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No. 7. Renard: Sur l'origine de l'acide borique trouvé dans les cendres des produits végétaux belges.
„ — Bruyne: De quelques organismes inférieurs nouveaux.
„ 8. Dewalque: Etat de la végétation, le 21 mars et le 21 avril 1889, à Gembloux, à Huccorgne, à Liège et à Spa.
„ 11. Longchamps: Sur l'effeuillaison à Longchamps-sur-Geer en 1889.
„ 12. Mac Leod: Expériences de culture concernant *Matthiola annua* et *Delphinium ajacis*.
„ — Vandenberghe: Etude des graines et de la germination des salicornes de Heyst et de Terneuzen.

Bulletin de la Société Royale Linnéenne de Bruxelles. T. XV (*continued*)

Livr. 5 and 6.

LOUIS: Du rôle physiologique de la feuille dans la végétation et dans la production du fruit.

—— – : Etude de la fleur, son origine et ses rapports avec l'arboriculture fruitière (continued in Livr. 7 and 8).

CARRON ET ZWENDELAAR: La florule des environs de Bruxelles (*continued*), (continued in Livr. 7–10).

Livr. 7 and 8.

LETTER: Herborisations aux environs de Givet.

Livr. 9 and 10.

De l'origine des maladies des végétaux et plus spécialement des arbres fruitiers.

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VAN BAMBEKE: Recherches sur la morphologie du *Phallus impudicus*, L. (Pl. I–III.)

CRÉPIN: Considérations sur quelques faits concernant le genre *Rosa*.

SACCARDO: Mycetes Sibirici. (Pl. IV–VI.)

Illustration horticole. Tome XXXVI (*continued*).

Livr. 6. DELCHEVALERIE: L'Horticulture dans l'Afrique centrale.

„ — Plates and descriptions of *Passiflora triloba*, Ruiz. et Pav. and *Begonia peltata*, Otto, var.

„ — Plates and descriptions of *Anthurium Scherzerianum*, Schott, var. *Mlle Lucienne Linden*, and *Adiantum tetraphyllum*, H. B. var. *obtusum*, M. Kuhn.

„ 8. Plates and descriptions of *Vriesea hybrida versaliensis*, Hort. and Varieties of *Gloxinia*.

Lindenia (J. Linden).

Vol. IV, Livr. 9-12, contains plates of—*Odontoglossum Bleichröderianum*, J. & L. Lind.; *O. Pescatorei*, var. *Lindenianum*; *O. Rossi*, var. *Mommianum*; *O. Warocqueanum*, J. & L. Lind.; *Zygopetalum Gibeziae*, N. E. Br.; *Masdevallia Shuttleworthii*, Rchb. f.; *Dendrobium Brymerianum*, Rchb. f.; *Odontoglossum Halli*, Lindl. var. *Lindeni*; *Cattleya Mossiae*, var. *Bousiesiana*; *Cypripedium Elliottianum*, J. O'Br.; *Dendrobium densiflorum*, Wall.; *Phajus grandiflorus*, Lour.; *Thunia Marshalliana*, Rchb. f.; *Laelia majalis*, Lindl.; *Anguloa Clowesi*, Lindl.; *Cattleya Mossiae*, var. *Warocqueana*.

Vol. V, Livr. 1–4, contains plates of—*Laelia elegans*, Morr.; *Dendrobium Paxtoni*, Lindl.; *Bolbophyllum Lobbi*, Lindl.; *Epidendrum vitellinum*, Lindl.; *Catasetum macrocarpum*, Rich. var. *chrysanthum*; *Calanthe Masuca*, Lindl.; *Dendrobium infundibulum*, Lindl.; *Epidendrum prismatocarpum*, Rchb. f.; *Miltonia vexillaria*, var. *superba*; *Oncidium Marshallianum*, Rchb. f.; *Miltonia Blunti*, Rchb. f. var. *Lubbersiana*; *Vanda Kimballiana*, Rchb. f.; *Oncidium concolor*, Hook.; *Cypripedium* × *orphanum*, Rchb. f.; *Dendrobium crumenatum*, Swartz; *Gongora maculata*, Lindl.

DENMARK.

Tidsskrift, Botanisk. (Copenhagen.) Bd. XVII, 3 Haeft.

RAUNKJAER: Myxomycetes Daniae (Fortsaettelse).

————: English description of some new and unsatisfactorily known species described in above treatise.

————: Notes on the vegetation of the North-Frisian Islands, and a contribution to an eventual flora of these islands.

————: Nogle Jagttagelser over Planter med forskjellig formede Blomster.

PETERSEN: Agaricineer, jagttagne i Omegnen af Slagelse.

BØRGESEN: Et lille Bidrag til Bornholms Desnude-Flora (Tav. 6).

————: Summa dissertat. praeced. Latine versa.

BRUUN: Jagttagelser over Løvspring, Blomstring, Frugtmodning og Løvfald i Veterinaer- og Landbohøjskolens Have i Aarene 1882–86.

JENSEN: Zostera's Spising (germination) with Résumé in French.

LANGE: Sur la synonymie du *Brassica lanceolata*, Lge.

KLÆRSKOU: Er *Brassica oleracea*, L. nogensuide funden vild voxende i Danmark?

————: Myrtaceae ex India occidentali a dominis Eggers, King, Sintenis, Stahl aliisque collectae.

WARMING: Biologiske Optegnelser om grønlandske Planter, 3.

ROSTRUP: Mykologiske Meddelelser.

PETIT: Sur une nouvelle espèce de *Bryonia*.

FRIDERICHSEN OG GELERT: One *Rubus commixtus* og naerstaaende Former.

FRANCE.

Actes de la Société Linnéenne de Bordeaux.

Tome II (*continued*). Livr. 3.

DEBEAUX: Synopsis de la flore de Gibraltar (suite).

Tome III. Livr. 1 and 2.

PETIT: Nouvelles recherches sur le pétiole des Phanérogames.

Annales de l'Institut Pasteur. Tome III.

No. 6. ROUX ET TERSIN: Contribution à l'étude de la diphthérie, II.

„ — MELCHINKOFF: Études sur l'immunité.

„ — CADEAC ET MEUNIER: Recherches sur l'action antiseptique des essences.

„ 7. LAURENT: Recherches sur la valeur comparée des nitrates et des sels ammoniacaux comme aliment de la levure de bière et des quelques autres plantes.

„ — DUCLAUX: Sur la conservation des levures.

„ 8. LUCET: Sur une nouvelle septicémie du lapin.

„ — DUCLAUX: Sur la nutrition intracellulaire, II.

„ 9. KRASILTSCHICK: Sur la symbiose de pucerons avec des bactéries.

„ 10. KAYSER: Action de la chaleur sur les levures.

„ — GAMALEIA: *Vibrio melchnikovi*; vaccination chimique.

„ — DUCLAUX: Note sur la formation des spores dans la levure.

„ 11. GAMALEIA: *Vibrio melchnikovi*; exaltation de sa virulence.

Annales de Micrographie (Paris), XII. Année (*continued*).

No. 10. DOWDESWELL: Sur une nouvelle espèce de microbe chromogène, le *Bacterium rosaceum metalloides* (suite).

,, — FREUDENREICH: Notes sur l'action du bacille pyocyanique sur la bactéridie charbonneuse.

,, — ————————: De l'action antiseptique de quelques essences sur les bacilles de la tuberculose, du charbon et du choléra.

,, 12. FORSTETTER: Un nouveau procédé d'analyse bactériologique de l'air.

Tome 2.

No. 1. FREUDENREICH: De l'antagonisme des Bactéries.

,, 2. KLEIN: Sur la morphologie des streptocoques.

,, 3. FREUDENREICH: De la teneur du lait en bactéries.

Annales des Sciences Naturelles. Botanique. Tom. IX (*continued*).

Nos. 4–6. FAYOD: Prodrome d'une histoire naturelle des Agaricinées (*continued*).

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Nos. 50–51. Traité Botanique (*suite*), pp. 273–336. Figs. 185–284.

Botaniste, Le. 1re Série (*continued*).

Fasc. 5. DANGEARD: Recherches de Morphologie et d'anatomie végétales. (Pl. VIII and IX.)

,, 6. ————: Essai sur l'anatomie des Cryptogames Vasculaires (2 Pl.)

Bulletin de la Société de Botanique de France. (Paris), Tome XXXVI.

No. 2. ROUY: Le *Silaus virescens*, Boiss. dans les Pyrénées orientales.

,, — CLOS: Le *Stachys ambigua*, Sm., est-il espèce, variété, ou hybride?

,, — JUMELLE: Marche de l'accroissement en poids des différents membres d'une plante annuelle.

,, — DEVAUX: Sur quelques modifications singulières observées sur des racines de graminées croissant dans l'eau.

,, — DANIEL: Structure anatomique comparée de la feuille et des folioles de l'involucre dans les corymbifères.

,, — LETOURNEUX: Note sur un voyage botanique à Tripoli de Barbarie.

,, — COSSON: Plantae in Cyrenaica et agro Tripolitano, anno 1875 a J. Daveau lectae.

,, — BLONDEL: Sur le parfum et son mode de production chez les roses.

Nos. 3–4. SZYSZYLOWICZ: Une excursion botanique au Monténégro.

,, — THOUVENIN: Sur l'appareil de soutien dans les tiges des Saxifrages.

,, — DANIEL: Structure comparée de la feuille et des folioles de l'involucre dans les Cynarocéphales et généralités sur les Composées.

,, — BORNET: Les Nostocacées heterocystées du Systema algarum de Agardh et leur synonymie actuelle.

,, — LE GRAND: Note sur le *Cyperus distachyos* et quelques autres espèces des Corbières.

,, — HUE: Lichenes yunnanenses a cl. Delavay praesertim annis 1886–87 collecti.

,, — ——: Lichenes yunnanenses.

,, — ——: Lichens du Cantal et de quelques départements voisins (continued in No. 5).

,, — GANDOGER: Plantes de Judée.

,, — BAINIER: Sur l'*Absidia cærulea*.

,, — MAURY: Sur la morphologie des tubercules du *Stachys affinis*, Bge.

Bulletin de la Société de Botanique de France (*continued*).

Nos. 3, 4. SEIGNETTE : Recherches anatomiques et physiologiques sur les 'Crosues du Japon.'

,, — JARDIN : Excursion botanique à 165 lieues du pole nord.

,, — GUIGNARD : Observations sur la structure et la division du noyau dans les cellules-mères du Pollen du Cycadées.

No. 5. SEIGNETTE : Notes sur les tubercules du *Spiræa filipendula* et du *Veratrum album*.

,, — ÉMERY : Épanouissement, veille et sommeil des périanthes.

,, — COSSON : Gramineae duae novae Tunetanae e genere *Sporobolus*.

,, — HUA : *Anemone nemorosa*, L. var. *anandra*.

,, — NIEL : Sur un phénomène remarquable de vitalité présenté par des souches de sapin.

,, — CARUEL : La Flora italiana et ses critiques.

,, — MANGIN : Observations sur la membrane du grain de pollen mûr.

,, — VALLOT : Causes physiologiques qui produisent le rabougrissement des arbres des cultures Japonaises.

,, — BASTIT : Comparison entre le rhizome et la tige feuillée des mousses.

,, — DANIEL : Structure anatomique comparée des bractées florales, des feuilles verticales et des feuilles engainantes.

,, — PONSON : Note sur un champignon rapporté au genre *Mylitta*.

,, — HY : Sur la présence en Anjou de l'*Equisetum littorale*, Kühlwein.

,, — LUIZET : Sur les Orchis hybrides, prov. de l'*Aceras anthropophora* et de l'*Orchis militaris*.

,, — CHABERT : Note sur la flore d'Algérie, II.

,, — EMERY : Sur la variation de l'eau dans les périanthes.

,, — DONNET-ADANSON : Note sur un sapin hybride.

,, — BRUNAUD : Champignons à ajouter à la flore mycologique des environs de Saintes.

,, — CAMUS : Localités nouvelles de plantes rares des environs de Paris.

,, — DEGAGNY : Origine nucléaire du protoplasma : sur l'origine des diastases dans la digestion du nucelle.

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BOUVET : Les *Rubus* de l'Anjou ; Essai d'une révision synthétique.

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No. 1. RENAULT : Notice sur les Sigillaires.

,, — TACNET : Etude sur les Blés et leur culture.

,, 2. NAUDIN : Les Tubercules des Légumineuses.

,, — BERTRAND ET RENAULT : Les Poroxylons.

,, — BOIS : Le Thé et ses succédanés.

,, — TACNET : Notice sur les plantes qui entrent dans la composition des prés et pâtures.

,, — GILLOT ET LUCAND : Catalogue raisonné des Champignons supérieurs.

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GODFRIN : Masse d'inclusion au savon ; application à la botanique, etc.

MACE : Sur la récupération de la vitalité des cultures de bactéries pa passage sur certains milieux.

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BEILLE: Essai sur les zones de végétation du massif central de la France.

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No. 5. ZEILLER: Empreintes végétales des couches de charbon de la Nouvelle-Calédonie.

„ — BLEICHER ET FLICHE: Tufs quaternaires du Nord-Est de la France.

„ — ZEILLER: Variations de formes du *Sigillaria Brardi*.

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Fasc. 1. ROLLAND: Essai d'un Calendrier des champignons comestibles des environs de Paris. (Pl. I–V.)

„ — QUINCY: *Lactarius pallidus*, Pers. (un cas tératologique). (Pl. VI.)

„ — BERTRAND: Clef dichotomique du genre Amanite (Oronge) espèces recueillies dans les Vosges.

„ — LUDWIG: Une nouvelle espèce du genre *Batarrea*.

„ 3. PATOUILLARD: Le Genre *Gonoderma*. (Pl. X and XI.)

„ — ——————: Note sur la présence de Basides à la surface du chapeau des Polypores.

„ — ——————: Sur une nouvelle forme de Polypore à Hyménium vesiculaire.

„ — LEGUÉ: Liste des Hyménomycètes observés dans le Perche depuis 1889.

„ — RICHON: Deux espèces nouvelles de *Cephalotheca*. (Pl. XII and XIII.)

„ — COSTANTIN: Note sur la culture de quelques Champignons.

Bulletin de la Société Philomathique de Paris. (Paris.) Série 8. Tome I.

No. 2. LAVENIR: Régénération des vignes au moyen du renversement de la sève.

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No. 25. TRÉCUL: Réponse à la note de M. van Tieghem, 'Sur le pédicule de la racine des Filicinées.'

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No. 1. HECKEL: Sur les écailles et les glandes calcaires épidermiques des Globulariées et des Sélaginées.

„ — RENAULT: Sur les feuilles de *Lepidodendron*.

„ 2. GIARD: Sur une galle produite chez le *Typhlocyba rosæ*, L. par une larve d'Hyménoptère.

„ 3. GUÉBHARD: Sur les partitions anormales des frondes de fougères.

„ 4. COURMONT: Sur une nouvelle tuberculose bacillaire, d'origine bovine.

„ 5. DANGEARD: Etude du noyau dans quelques groupes inférieurs des végétaux.

„ — LESAGE: Influence du bord de la mer sur la structure des feuilles.

„ 6. CLAUDEL: Sur les matières colorantes du spermoderme dans les Angiospermes.

„ 7. SAPPEY: De l'appareil vasculaire des animaux et des végétaux, étudié comparativement par la méthode des coupes et par la méthode thermochimique.

„ 8. BERTHELOT: Remarques sur les conditions où s'opère la fixation de l'azote par les terres argileuses.

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No. 8. BERTHELOT : Recherches nouvelles sur la fixation de l'azote par la terre végétale. Influence de l'électricité.

,, — GAUTIER : Observations relatives à la communication précédente.

,, 9. SCHLŒSING : Sur les relations de l'azote atmosphérique avec la terre végétale. Réponse à M. Berthelot.

,, — VERNEUIL : Propriétés pathogènes des microbes contenus dans les tumeurs malignes.

,, — HECKEL ET SCHLAGDENHAUFFEN : Sur la sécrétion oléo-gommo-résoneuse des Araucarias.

,, 10. VILLE : Recherches sur les relations qui existent entre la couleur des plantes et la richesse des terres en agents de fertilité.

,, — TIMIRIAZEFF : La protophylline dans les plantes étiolées.

,, 11. BERTHELOT : Sur la fixation de l'azote atmosphérique.

,, — ———— : Observations sur la formation de l'ammoniaque et de composés azotés volatils, aux dépens de la terre végétale et des plantes.

,, — SCHLŒSING : Sur la nitrification de l'ammoniaque.

,, — PÉCHARD : Influence, dans les terres nues, du plâtre et de l'argile, sur la conservation de l'azote, la fixation de l'azote atmosphérique et la nitrification.

,, 12. ARLOING : Détermination du microbe producteur de la péripneumonie contagieuse du bœuf.

,, — GASTINE : Sur la fermentation alcoolique des miels et la préparation de l'hydromel.

,, 13. RIMELIN : Sur la cause probable des partitions frondales des Fougères.

,, 15. CHAUVEAU : Sur le transformisme en microbiologie pathogène. Des limites, des conditions et des conséquences de la variabilité du *Bacillus anthracis* (continued in No. 16).

,, — MANGIN : Sur la présence des composés pectiques dans les végétaux.

,, 16. SCHLŒSING FILS : Sur l'atmosphère confinée dans le sol (continued in No. 18).

,, 17. VILLE : Recherches sur les relations qui existent entre les caractères physiques des plantes et la richesse du sol en éléments de fertilité.

,, — MUNTZ : Sur le rôle de l'ammoniaque dans la nutrition des végétaux supérieurs.

,, 18. SAPORTA : Sur quelques hybrides observés dernièrement en Provence.

,, — BRÉAL : Fixation de l'azote par les Légumineuses.

,, 19. MANGIN : Sur les modifications apportées, dans les échanges gazeux normaux des plantes, par la présence des acides organiques.

,, 20. LECHARTIER : Sur l'incinération des matières végétales.

,, — LINOSSIER ET ROUX : Sur la morphologie et la biologie du champignon du muguet.

,, 22. DEHERAIN : Sur l'épuisement des terres par la culture sans engrais, et l'utilité de la matière organique du sol.

,, 23. ARLOING : Recherches sur les diastases sécrétées par le *Bacillus hemine-crobio-biophilus* dans les milieux de culture.

,, — FLICHE : Sur les bois silicifiés d'Algérie.

,, — GAUDRY : Observations à propos la dernière communication.

,, 24. SCHLŒSING : Sur la nitrification de l'ammoniaque.

,, — TAURET : Sur deux sucres nouveaux retirés du québracho (*Aspidosperma quebracho*).

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„ — THÉLOHAN: Sur la constitution des spores des Myxosporidies.

„ — THIL ET THOUROUDE: Sur une étude micrographique du tissu ligneux dans les arbres et arbrisseaux indigènes.

„ — HERMENT: Note relative aux arbres silicifiés de l'Algérie.

„ 25. CLOS: De la production de lamelles de glace à la surface de l'aubier de certaines espèces de plantes.

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No. 25 BABÈS: Note sur quelques matières colorantes et aromatiques produites par le bacille pyocyanique.

„ 26. PORCET: Note sur les microbes de l'eau de Vichy.

„ — OLIVIER: Sur le bacille de la fièvre typhoïde.

„ — RODET: De l'importance de la température dans la détermination des espèces microbiennes en général, et spécialement du bacille typhique.

„ 27. OLIVIER: Sur la culture du bacille de la fièvre typhoïde dans les eaux des égouts.

„ 28. ROUX: Sur la culture des bactéries et particulièrement des streptocoques, dans les milieux au touraillon.

„ 29. COURMONT: Deuxième note sur un nouveau bacille tuberculeux trouvé chez un bœuf.

„ 30. ROGER: De la production par les microbes pathogènes de substances solubles qui favorisent leur développement.

„ 35. BOSSANO ET STEULLET: Résistances des germes tétaniques à l'action de certains antiseptiques.

„ — CHARRIN: Evolution des microbes chez les animaux vaccinés.

„ — BRANDZA: Sur l'anatomie et le développement des téguments de la graine des Lins.

„ 36. BONNIER: Note sur quelques plantes à chlorophylle qui ne dégagent pas d'oxygène à la lumière.

„ 38. LEROY: Contribution à l'étude biologique du microbe de l'érysipèle.

„ — COMBEMALE ET DUBIQUET: Recherches sur l'action physiologique de l'écorce de tige de sureau (*Sambucus nigra*).

„ 41. COURMONT: Substances solubles favorisantes fabriquées par un bacille tuberculeux.

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No. 12. LUIZET: Herborisation à Fontainebleau.

„ — KARSTEN ET HARIOT: Fungi nonnulli Gallici.

„ — LECLERC: Sur l'endoderme de la tige des Sélaginelles.

„ — MAURY: Enumération des plantes du Haut Orénoque récoltées par MM. Chaffanjon et Gaillard (*continued*) (continued in Nos. 15, 16).

„ 13. FLAHAULT: Les herborisations aux environs de Montpellier (*continued*).

„ — GUIGNARD: Observations sur le pollen des Cycadées (continued in No. 14).

„ — DRAKE: Note sur une Thyméléacée nouvelle du Tonkin.

„ 14. ———: Contribution à la flore de l'Amérique équatoriale. Note sur les plantes récoltées par M. Poortman en 1881–2 (*concluded*).

„ — COSTANTIN: *Echinobotryum* et *Stysanus* (continued in No. 15).

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No. 14. MASCLEF : Etudes sur la Géographie botanique du nord de la France (*continued*).
„ — PATOUILLARD : Fragments mycologiques (*continued*).
„ 16. VLADESEN : Communications préliminaires sur la st cture de la tige des Sélaginelles.
„ — HARIOT : Note sur le genre *Cephaleuros*.

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No. 10. SMITH, H. L. : Contribution à l'histoire naturelle des Diatomées (*fin*).
„ 17. GIARD : Castration parasitaire de l'*Hypericum perforatum*.
„ — BRUN : A propos des Diatomées fossiles du Japan.

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„ — BERGMAN : Les Orchidées de Semis ; Les Cattleyas.
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„ — BERGMAN : Les Orchidées de Semis (continued in No. 103 bis).
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„ 103. ROLFE : *Cymbidium madidum*, Lindl.
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„ — PHILIBERT : *Orthothecium Duriæi*.
„ — AMANN : *Bryum Comense—Campylopus alpinus*—Musci novi rhætici—*Brachythecum trachypodium* — Études bryologiques — Neuf mousses nouvelles pour la Suisse.
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„ 82. LAGRAVE ET MARÇAIS: Essai monographique sur les espèces françaises du genre *Heracleum* (continued in No. 83).

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„ — HUE: Revue des travaux sur la description et la géographie botanique des lichens, publiées en 1888.
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„ — FRANCHET: Revue des travaux sur la botanique descriptive et la géographie botanique des plantes de l'Asie, publiées en 1888.
„ 9. COSTANTIN: Sur les variations des *Alternaria* et des *Cladosporium* (Fig. 58, and Pl. 23 and 24).
„ — DUFOUR: Les nouveaux procédés de gravure photographique.
„ — JUMELLE: Revue des travaux de physiologie végétale parus en 1888 et jusqu'en juillet 1889.

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„ — BONNET: Du parasitisme de la Truffe et de la couleur de son mycélium.
„ — ROUMEGUÈRE: Fungi selecti et siccati, Centurie L°.
„ — SOROKINE: Matériaux pour la Flore cryptogamique de l'Asie centrale (continued in No. 44).
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„ — ROUMEGUÈRE: Fungi selecti exsiccati, Centure LI°.
„ — SACCARDO ET BERLÈSE: Fungi Guinenses.
„ — KARSTEN: Aliquot species novae fungorum.
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No. 7. DUMAS-DAMON: Bryologie du département du Puy-de-Dôme (suite).
„ — BUYSSON: Monographie des cryptogames vasculaires d'Europe—Filicinées.
„ 9–10. RENOUX: Nouvelle contribution à la flore bourbonnaise (continued in No. 11).

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AUGÉ: Rapport sur la Sériciculture.

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„ 5. GRIEPENKERL: Die Versteinerungen der senonen Kreide von Königslutter im Herzogthum Braunschweig Plantae, p. 14.

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„ 2. CRIÉ: Beiträge zur Kenntniss der fossilen Flora einiger Inseln des Südpacifischen u. Indischen Oceans (10 Taf.).

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„ — MÜLLER: Abweichend gebildete Blumen von Marica (with Woodcut).

„ — KNY: Umkehrversuche mit *Ampelopsis quinquefolia* u. *Hedera Helix*.

„ — WIELER: Erwiderung auf R. Hartig's Bemerkungen zu meiner Abhandlung 'Ueber den Ort der Wasserleitung im Holzkörper,' etc.

„ — BECK: Ueber die Sporenbildung der Gattung *Phlyctospora*, Corda (with Woodcut).

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„ — THOMAS: *Synchytrium alpinum*, n. sp.

„ — SAPOSCHNIKOFF: Die Stärkebildung aus Zucker in den Laubblättern.

„ 6. CORRENS: Culturversuche mit dem Pollen von *Primula acaulis*, Lamk.

„ 7. BOKORNY: Eine bemerkenswerthe Wirkung oxydirter Eisenvitriollösungen auf lebende Pflanzenzellen.

„ — ———: Ueber den Nachweis von Wasserstoffsuperoxyd in lebenden Pflanzenzellen.

„ — WAHRLICH: Anatomische Eigenthümlichkeit einer Vampyrella (Plate X).

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„ 8. WETTSTEIN: Untersuchungen über *Nigritella angustifolia*, Rich. (Taf. XIII).

„ — JÄNNICKE: Gekeimte Samen in Früchten von *Impatiens longicornis*, Wall.

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„ — REISS: Ueber die Natur der Reservecellulose u. über ihre Auflösungsweise bei der Keimung der Samen.

„ — PALLA: Ueber Zellhautbildung u. Wachsthum kernlosen Protoplasmas.

„ — FRANK: Ueber die Pilzsymbiose der Leguminosen.

„ — TISCHUTKIN: Die Rolle der Bacterien bei der Veränderung der Eiweissstoffe auf den Blättern von *Pinguicula*.

„ — SCHULZE: Ueber die stickstofffreien Reservestoffe einiger Leguminosensamen.

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————: Zur Biologie der zahmen Rebe.

————: Ueber die künstliche Besiedelung einer Pflanze mit Ameisen.

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KLEIN: Ueber einen neuen Typus der Sporenbildung bei den endosporen Bacterien (Taf. XII).

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„ 15. KELLER: Die Transpiration der Pflanzen u. ihre Abhängigkeit von äussern Bedingungen.

„ 16. GODLEWSKI: Ueber die biologische Bedeutung der Etiolierungserscheinungen.

„ 18. SCHIEMENZ: Parasitische Schnecken (continued in No. 19).

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„ 35. Blocki: *Rosa gypsicola*, n. sp.

„ 37. Röll: Die Torfmoss-Systematik u. die Descendenz-Theorie (continued in No. 38).

„ — Blocki: *Rosa thyraica*, n. sp.

„ 39. Loew und Bokorny: Ueber das Verhalten von Pflanzenzellen zu stark verdünnter alkalischer Silberlösung, II (continued in Nos. 45 and 46).

„ 40. Hesse: Zur Entwickelungsgeschichte der Hymenogastreen, *Leucogaster floccosus* (continued in No. 41).

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„ — Keller: Das Potentillarium des Herrn A. Siegfried in Winterthur (continued in Nos. 46–48).

„ 46. Blocki: *Rosa Knappii*, n. sp.

„ 48. Bennett, A. W.: Note on cryptogamic terminology.

„ — Knuth: Die Bestäubungseinrichtung von *Eryngium maritimum*, L. u. *Cakile maritima*, L.

„ 49. Rostowzew: Ein interessanter Wohnort wilder Planzenformen.

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„ — Buchner: Ueber die bakterientödtende Wirkung des zellenfreien Blutserums (*Schluss*).

„ 2. Ali-Cohen: Eigenbewegung bei Mikrokokken.

„ — Beyerinck: Die Lactase, ein neues Enzym (m. 2 Fig.).

„ 3. Arustamoff: Zur Frage über die Entstehung der typhösen Pneumonie (continued in No. 4).

„ — Karlinski: Untersuch. über das Verhalten der Typhusbacillen in typhösen Dejektionen.

„ 5. Ludwig: Weitere Mittheil. über Alkoholgährung u. die Schleimflüsse lebender Bäume (continued in No. 6).

„ — Protopopoff: Ueber die Hauptursache der Abschwächung des Tollwuthgiftes.

„ 6. Zarniko: Zur Kenntniss des Diphtheriebacillus (continued in No. 7–8).

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No. 11. Karlinski: Zur Kenntniss des *Bacillus enteritidis*, Gärtner.

„ 12. Klein: Botanische Bakterienstudien, I (mit 3 Taf.) (continued in Nos. 13 and 14).

„ 15. Czaplewski: Zur Anlage bakteriologischer Museen.

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No. 21. Mendoza: Zur Eigenbewegung der Mikrokokken.

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No. 22. KLEIN: Ein weiterer Beitrag zur Kenntniss des Bacillus der Grouse-disease.
„ — MENGE: Ueber rothe Milch.
„ — VIQUERAT: Einfacher, kupferner Sterilisirapparat.
„ 23. BUJWID: Ueber die Reinkultur des *Actinomyces*.
„ — PETRUSCHKY: Bacterio-chemische Untersuch. (continued in No. 24).
„ 25. FRAENKEL: Zur Lehre von der Identität des *Streptococcus pyogenes* u. *S. erysipelatos*.

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„ — MÜLLER, F.: Freie Gefässbündel in den Halmen von *Olyra*.
„ — TAUBERT: Leguminosæ novæ v. minus cognitæ austro-americanæ.
„ 5. SCHMITZ: Systematische Uebersicht der bisher bekannten Gattungen der Florideen (Taf. XXI).
„ — KÜHN: Untersuchungen über die Anatomie der Marattiaceen u. anderer Gefässkryptogamen.
„ — MÜLLER, J.: Lichenologische Beiträge, XXXII.
„ — ———: Lichenes argentinienses.

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Heft 13. WITTMACK UND GRAEBENER: *Lobelia laxiflora*, H. B. K. (Taf. 1301.)
„ — GOESCHKE: *Pinus Peuce*, Griseb. (Fig. 55.)
„ — WITTMACK: *Vriesea* × *Magnisiana*, Kettel et Wittm., n. hyb.
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„ — LEHMANN: Mittheilungen über *Odontoglossum vexillarium*.
„ 14. PHILIPPI: Drei neue Monocotyledonen: 1. *Latace Volckmanni*, Philippi; 2. *Tillandsia Geissei*, Phil.; 3. *Stemmatium narcissoides*, Phil.
„ — KRÄNZLIN UND WITTMACK: *Odontoglossum Brandtii*, Kr. et Wittm., n. sp.
„ 15. BRANDT: *Canna indica*, hyb. (Taf. 1303.)
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„ 17. SPRENGER: *Ceratotheca triloba*, E. M., vel. *Sporledera Kraussiana*, Bernh. (Taf. 1305.)
„ — DRUDE UND BRANDT: *Cocos australis*.
„ 18. REGEL: *Cattleya Nilsoni*, Sander., n. hyb.
„ — ——: *Agave Maximowiczziana*, Rgl.
„ — KÜHN: Die Monstre-Veredelungen.
„ — *Sarracenia Wrigleyana*, hyb. (Fig. 75.)
„ 19. REGEL: Zwei neue Tulpen aus Buchara: 1. *Tulipa Maximowiczi*, Rgl.; 2. *T. Batalini*, Rgl. (Taf. 1307.)
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„ 20. KRÄNZLIN: *Odontoglossum Brandtii*, Kr. et Witttm., n. sp. (Taf. 1308.)
„ 21. SCHUMANN, K.: *Crinum Schimperi*, Vatkems. (Taf. 1309.)

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„ — SIEHE: *Grewia parviflora*, Bge.
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„ — SIEHE: *Shepherdia argentea*, Nutt. (Fig. 89.)
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„ 24. SPRENGER: *Lachenalia quadricolor*, Jacq., var. *praecox*, Sprenger. (Taf. 1312, Fig. 1.)
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„ — DIETEL: Ueber das Vorkommen von *Puccinia perplexans*, Plow., in Deutschland.
„ — MAGNUS: Notiz zu Dietel's Mittheil. über die Puccinien auf *Asphodelus*.
„ — BLONSKI: Fungi polonici novi.
„ 5. REHM: Exotische Ascomyceten, I.
„ — WARNSTORF: Ueber das Verhältniss zwischen *Sphagnum imbricatum*, (Hornsch.) Russ., *Sph. Portorisense*, Hpe., u. *Sph. Herminieri*, Schpr.
„ — MÖBIUS: Bearbeitung der von H. Schenck in Brasilien gesammelten Algen.
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„ — OUDEMANS: *Trichophila*, n. gen.
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„ — HUTH: Ueber Pepsin-Pflanzen.
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„ — LOEBEL: Anatomie der Laubblätter, vorzüglich der Blattgrün führenden Gewebe (Taf. II und III).
„ — MÜLLER, N. J. C.: Spectralanalyse der Blüthenfarben (Taf. IV–VI),
„ — RODEWALD: Weitere Untersuchungen über den Stoff- und Kraftumsatz im Athmungsprocess der Pflanze.
„ — RÖSELER: Das Dickenwachsthum und die Entwickelungsgeschichte der secundären Gefässbündel bei den baumartigen Lilien (Taf. XIII–XVI).
„ — SCHENCK: Ueber das Aerenchym. ein dem Kork homologes Gewebe bei Sumpfpflanzen (Taf. XXIII–XXVIII).
„ — SCHUMANN: Blüthenmorphologische Studien (Taf. XVII).
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„ — LÜDTKE: Beiträge zur Kenntniss der Aleuronkörner (Taf. II–IV).
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——— : Ueber Prof. Williamson's mikroskopische Präparate von Pflanzen der Kohlenformation.

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„ — ERCK: Beobachtungen u. Bemerkungen über die Capreaceen u. deren Bastarde.
„ — FIGERT: Botanische Mittheilungen aus Schlesien, II.
„ — SAGORSKI: Berichtigungen zur Flora von Thüringen.
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„ — v. KELLER: Die Rosen von Trsztenna u. der niederen Tatra in Ungarn.
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„ — WIEFEL: Ein Digitalis-Bastard in Thüringen.
„ — REICHERT: Zur Flora von Leipzig.
„ 7. SAGORSKI: Plantae criticae Thuringiae, IV.
„ — ERCK: Über die Capreaceen u. deren Bastarde.
„ — TÖPFFER: Gastein u. seine Flora, II.
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„ — MARSSON: Über *Bromus laxus*, Hornemann.
„ — v. SEEMEN: *Salix purpurea* × *fragilis* = *Salix Margaretæ*.
„ — SCHEUERLE: Schleichers 86 'Arten' der *Salix nigricans* (continued in Nos. 9–10).

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„ — SAGORSKI: Das Haussknechtsche *Hieracium chlorocephalum* von Thüringen.
„ — ————: Die Rosen der Hohen Tatra u. der nächsten Umgebung (continued in Nos. 11 and 12).
„ — KNUTH: Die Frühlingsflora der Insel Sylt (continued in Nos. 11 and 12).
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„ — ————: Der Hangelstein bei Giessen.
„ — FIGERT: *Carex Beckmanniana*, ein neuer Bastard in Schlesien.

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„ 50. HEGELMAIER: Ueber den Keimsack einiger Compositen u. dessen Umhüllung (continued in Nos. 51 and 52).

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Academy, The. 1889. No. 892.

TYLOR: The fertilisation of the Date Palm in ancient Assyria.

Album, The Orchid.

Vol. VIII (*continued*) contains plates of—*Phajus maculatus*, Lindl.; *Odontoglossum Schröderianum*, Rchb. f.; *Lælia superbiens Quesneliana*, Hort.; *Lycaste costata*, Lindl.

Vol. IX contains plates of—*Cattleya Mastersoniæ*, Rchb. f.; *Bifrenaria aurantiaca*, Lindl.; *Odontoglossum Alexandræ Wilsonii; Cattleya Eldorado virginalis; Cypripedium Arthurianum*, Rchb. f.; *Odontoglossum cuspidatum xanthoglossum*, Rchb. f.; *Cypripedium macropterum*, Rchb. f.; *Oncidium anthocrene*, Rchb. f.; *Lælia elegans Blenheimense; Pescatoria cerina*, Rchb. f.; *Lælia monophylla*, N. E. Brown; *Dendrobium transparens*, Wall.

Annals of Botany. Vol. III.

No. X. HOOKER: *Pachytheca.* (Pl. VIII.)

BARBER: The structure of *Pachytheca.* (Pl. IX.)

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GROOM: On the function of Lacticiferous tubes. (Pl. XI.)

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No. X. JOHNSON: The nursing of the embryo and some other points in *Myzodendron punctulatum*, Banks et Sol. (Pl. XIII, XIV.)

FULTON: The dispersion of the spores of Fungi by the agency of insects, with special reference to the *Phalloidei*. (Pl. XV.)

BOWER: On the pitcher of *Nepenthes*: A study in the morphology of the leaf. (Pl. XVI.)

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VINES: On the Mechanism of Stomata.

No. XI. SCOTT AND BREBNER: On the Anatomy and Histogeny of *Strychnos*. (Pl. XVIII, XIX.)

BOWER: The comparative examination of the meristems of Ferns as a Phylogenetic study. (Pl. XX–XXIV.)

VINES: On Epinasty and Hyponasty. (Woodcut 7.)

Notes—ERNST: On two cases of Laminar enations from the surfaces of leaves.

LOWE: On the propagation of Ferns.

SCOTT: The distribution of Laticiferous tissue in the leaf.

Record of Current Literature for Jan.—June, 1889.

Bulletin of Miscellaneous Information. Kew, 1889 (*continued*).

No. 33. Flowers of *Calligonum* as an article of Food in N.-W. India.
,, — Earliest notice of Coca.
,, — Buazé fibre (*Securidaca longipedunculata* Fres.).
,, — Vegetable productions, Central China.
,, — Vine cultivation in the Gironde.
,, 34. Bahia piassava (*Attalea funifera*, Mart.).
,, — Seedlings of Sugar Cane at Barbados (*Saccharum officinarum*).
,, — Cinchona in Jamaica.
,, — Gambier (*Uncaria Gambier*, Roxb.).
,, — Fibre industry at the Bahamas (*Agave rigida* var. *Sisalana*).
,, 35. Collecting and preserving fleshy fungi.
,, — Oil palm in Labuan (*Elaeis guineensis*).
,, — Ramie or *Rhea* (*Boehmeria nivea*, Hk. and Arn.) (continued in No. 36).
,, 36. Poisoning from Turnsole in Persia (*Chrozophora tinctoria*, A. Juss.).
,, — Food grains of India (*continued*) (*Dendrocalamus strictus*, Nees).
,, — Cool cultivation of tropical and sub-tropical plants.

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,, 132. ROLFE: *Cypripedium de Witt Smith*, n. hyb.
,, — ———: *Odontoglossum Wendlandianum* × hyb. nat.
,, — *Rosa berberidifolia* (Figs. 1 and 2) (see also No. 134).
,, — BROWN: *Dendrobium crystallinum*, Rchb. f.
,, — ROLFE: *Orchis latifolia-maculata*.
,, — *Rosa gigantea* (Fig. 4).
,, 133. BAKER: *Ornithogalum* (*Cathissa*) *apertiflorum*, Baker, n. sp.
,, — ———: *Fritillaria* (*Monocodon*) *hericaulis*, Baker, n. sp.
,, — ROLFE: *Odontoglossum Harryanum*, var. *flavescens*, n. var.
,, — ———: *Cattleya inbricata* × Rchb. f.

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No. 133. JACKSON: Chinese White Wax.
„ — W. B.: Angræcums.
„ 134. BURBIDGE: The nomenclature of Orchids and other plants.
„ — BROWN: Two new aroids.
„ — ROLFE: *Odontoglossum Hummewellianum*, n. sp.
„ — ———: List of Garden Orchids (*continued*) (continued in Nos. 137, 143, 144).
„ 135. ———: *Acineta Chrysantha*, Lindl.
„ — BAKER: *Albuca* (*Eualbuca*) *trichophylla*, Baker, n. sp.
„ — ROLFE: *Dendrobium transparens alba*, n. var.
„ — Report on the condition of the fruit crops.
„ — Unconscious influence of human agency on the flora of Scotland.
„ 136. HENSLOW: Colour in plants (continned in Nos. 137–139).
„ — M. T. M.: *Spiræa Kamtschatika.*
„ 137. ROLFE: *Masdevallia Ellisiana* × n. hyb.
„ — BAKER: *Gladiolus Leichtlini*, Baker, n. sp.
„ — BURBIDGE: *Narcissus juncifolio* × *muticus* (Fig. 22).
„ — NORMAN: American Cypripediums.
„ 138. GUMBLETON: *Gladiolus Turicensis* ×.
„ — ROLFE: *Luddemannia Pescatorei*, Linden and Rchb. f.
„ — W. R.: Insect pests.
„ — ROLFE: *Mormodes luxatum*, Lindl.
„ — W. B.: *Spathoglottis Vieillardii.*
„ — ROLFE: *Cynoches pentadactylon*, Lindl. (Fig. 26).
„ 139. BROWN: *Eulophia bella*, N. E. Br., n. sp.
„ — ———: *Montbretia securigera*, DC.
„ — DOUGLAS: The potato disease.
„ 140. VEITCH: Orchid culture past and present (continued in No. 141).
„ — BROWN: *Phajus Philippinensis*, N. E. Br., n. sp.
„ — ROLFE: *Masdevallia coccinea*, Linden.
„ — BROWN: *Dendrobium polyphlebium* and var. *Emerici* (Fig. 33).
„ — Peloria in Larkspur (Fig. 35).
„ 141. BROWN: *Cypripedium* 'Beatrice,' n. hyb.
„ — *Montbretia securigera*, fertilisation of.
„ — Branching palms (with Fig. of *Phœnix sylvestris*).
„ 142. P. E. N.: A history of English gardening (*continued*).
„ — ROLFE: *Vanda Kimballiana*, Rchb. f.
„ — ———: *Oncidium Retemeyerianum*, Rchb. f.
„ — W. B.: *Cypripedium niveum* and allies.
„ — D. D.: *Podophyllum pleianthum*, Hance, n. sp. (Fig. 44).
„ — BROWN: *Eulophia callichroma*, Rchb. f.
„ — Dispersal of the fruit of Pharus.
„ 143. D. D.: *Tigridia Pringlei*, Wats.
„ — ROLFE: *Lælio-Cattleya* × *Stella*, n. hyb.
„ — ———: *Bulbophyllum saltatorium*, Lindl.
„ — The mountains of New Guinea.
„ 144. BROWN: *Watsonia iridifolia*, Ker. var. *O'Brieni*, N. E. Br., n. var.
„ — D. D.: *Primulina tabacum*, n. sp.

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„ 145. ROLFE : *Lælio-Cattleya* × *aurora*, n. hyb.
„ — J. VAN V. : The origin of cultivated plants.
„ — ROLFE : *Dendrobium lineale*, n. sp.
„ — *Satyrium coriifolium*.
„ 147. BAKER : *Sanseviera subspicata*, Baker, n. sp.
„ — Proliferous raspberry (Figs. 62–64).
„ 148. ROLFE : *Cypripedium Minerva*, n. hyb. The female of *Catasetum Bungerothii*.
„ — New Ferns.
„ — WEATHERS : Edible Fungi.
„ — O'BRIEN : *Phœnix Rœbelenii*.
„ 149. *Nepenthes Burkeii*, Mast. (Fig. 69).
„ — ROLFE : *Aganisia cyanea ; Cattleya Dowiana aurea* with rosy segments.
„ 150. HEMSLEY : The history of the Chrysanthemum (continued in Nos. 151, 152, and 154).
„ — BAKER : *Aloe* (*Eualoe*) *Monteiroi*, Baker, n. sp.
„ — PHELPS : Direct influence of Pollen on the Orange.
„ 151. BAKER : *Adiantum paradiseæ*, Baker, n. sp.
„ — ROLFE : *Bulbophyllum fallax*, Rolfe, n. sp.
„ — BROWN, N. E. : Catasetums.
„ — ROLFE : *Cattleya Hardyana*, Williams; *Lælio-Catleya* × *Victoria*, Rolfe.
„ 152. ——— : *Lælio-Cattleya* × *elegans Cooksoni*, n. var.
„ — BAKER : Enumeration of the species of *Kniphofia*.
„ 153. ROLFE : *Lælio-Cattleya* × *Cassiope*, n. hyb. ; *Liparis fulgens*, Rolfe, n. sp.
„ — Chrysanthemum sport (Fig. 86).
„ 154. BROWN : N. E. : *Stapelia erectiflora*, n. sp.
„ — WILLIS : Potato scab experiments.
„ — DOUGLAS : Chrysanthemum sports.
„ — M. T. M. : *Nepenthes Curtisi* (Fig. 90).
„ 155. O'BRIEN : *Liparis Borokeri*, Harvey.
„ — BROWN, N. E. : *Stapelia Desmetiana*, n. sp.
„ — Leaf structure (Figs. 94 and 95).
„ 156. BAKER : *Massonia* (*Eumassonia*) *Amygdalina*, Baker, n. sp.
„ — ROLFE : *Cattleya Dowiana*, var. *Chrysotoxa*.
„ — HEMSLEY : The Chinese Tulip Tree.
„ 157. BROWN, N. E. : *Paulowilhelmia speciosa*, Hochst.

Gazette, Agricultural Students'. No. IV. Pt. II.

E. K. : Experiments on Pastures.
HARKER : A new enemy to plants (*Oligochaete*, sp.).
W.M.C. : Experimental Grass Plots.

Gossip, Science. 1889. (*continued.*)

No. 296. Botanical notes from the Swiss Highlands (*continued*), (over the Gemmi to Zermatt).
„ — HAMSON : *Schizanthus*, botanical Study.
„ — TANSLEY : The development of colours of flowers through insect-selection.

Gossip, Science (*continued*).

No. 296. BRYAN: A day among the salt marshes at Hunstanton.
„ — Botanical notes from West Cork; *Luzula albida* in Sussex; *Artemisia vulgaris* in Colorada; Monstrosity of *Plantago lanceolata*.
„ 299. COCKERELL: Insects and the colours of flowers.
„ 300. *Damasonium stellatum; Matthiola incana; Mercurialis perennis*, form *autumnalis*.

Grevillea. Vol. XVIII.

No. 85. COOKE: New Australasian Fungi (*continued* from Vol. XVII), (continued in No. 86.)
„ — ———: New British Fungi (*continued* from Vol. XVII), (continued in No. 86).
„ — MASSEE: British Pyrenomycetes (continued in No. 86).
„ — Synopsis Pyrenomycetum (continued in No. 86).
„ — Revision of Thelephoreae.
„ 86. COOKE: Some Exotic Fungi.
„ — CROMBIE: Index Lichenum Brittanicorum. Pt. II. (*continued* from Vol. XV.)

Icones Plantarum (Hooker's). Third Series. Vol. IX (*continued*).

Part II contains plates and descriptions of—*Pholidota calceata*, Rchb. f.; *P. protracta*, Hook. f.; *P. recurva*, Lindl.; *P. rubra*, Lindl.; *P. convallariae*, Hook. f.; *P. Griffithii*, Hook. f.; *Eulophia explanata*, Lindl.; *Tainia promensis*, Hook. f.; *Deinanthe bifida*, Maxim.; *Poliothyrsis sinensis*, Oliv.; *Liparis obscura*, Hook. f.; *L. Ridleyi*, Hook. f.; *L. resupinata*, Ridl.; *L. delicatula*, Hook. f.; *L. platyrachis*, Hook. f.; *Pholidota parviflora*, Hook. f.; *Tetracentron sinense*, Oliv.; *Toricellia angulata*, Oliv.; *Cercis racemosa*, Oliv.; *Saruma Henryi*, Oliv.; *Acer Henryi*, Pax.; *A. tenellum*, Pax.; (*A. sinense*, Pax.; *A. oliverianum*, Pax.; *A. cordatum*, Pax.; *A. erosum*, Pax.; *A. Maximowiczii*, Pax.; *A. Francheti*, Pax.; *A. tetramerum*; new species collected by Dr. Henry in China, descriptions only); *Dipteronia sinensis*, Oliv.; *Erythrospermum hypoleucum*, Oliv.; *Natsiatum sinense*, Oliv.

Journal of Botany. Vol. XXVII. (*continued*).

No. 319. BRITTEN: Heinrich Gustav Reichenbach.
„ — WILLIAMS: The Pinks of the Transvaal.
„ — DRUCE: Plants of Easterness and Elgin.
„ — WEST, W.: The Freshwater Algae of Maine.
„ — LINTON, E. F. AND W.-R.: New County Records for Skye, Ross, Sutherland, and Caithness.
„ — SAUNDERS: Notes on the Flora of S. Bedfordshire.
„ — BRITTEN AND BOULGER: Biographical Index of British and Irish Botanists (continued in No. 320).
„ — *Festuca heterophylla*, Lam. in Britain, *Gentiana amarella*, var. *praecox*.
„ 320. CARRINGTON AND PEARSON: A new Hepatic (with Plate 290).
„ — BEEBY: On some British *Viola* forms.
„ — MARSHALL: Notes on Highland plants.
„ — MURRAY, G.: Catalogue of the Marine Algae of the West Indian Region, (*continued*), (continued in Nos. 321–2).
„ — BENNETT, A.: The Synonymy of *Potamogeton rufescens*, Schrad.

Journal of Botany (*continued*).

No. 320. BRIGGS: *Orchis latifolio-maculata*, Towns. (?) in Devon. *Festuca heterophylla*, Lam. in Britain and in North Hants. A Perthshire Orchid, *Ranunculus acris*, L. Autumnal flowering of *Mercurialis perennis*. *Molinia cærulea*, in the Bristol Flora.

„ 321. BRITTEN: *Mundia*, Kth. v. *Mundtia*, Harv.

„ — BENNETT, A.: The Synonymy of *Potamogeton Tizii*, Roth.

„ — WHITE, F. B.: A list of British Willows.

„ — MCARDLE: Hepaticæ of Co. Wicklow.

„ — BAKER, J. G.: On a new species of *Polypodium* from Jamaica.

„ — CARRUTHERS: Report of the Department of Botany, British Museum, for 1888.

Hybrid Thistles near Plymouth, *Rubus rhenanus*, Müll.? *Melampyrum sylvaticum* in Gloucestershire, *Lophocolea spicata*, Tayl. in North Wales, New Bucks Plants, *Falcaria Rivini* in Kent, *Festuca heterophylla*, *Poa palustris*, L. in Britain.

No. 322. WEST: The Fresh-water Algae of North Yorkshire (Plate 291).

„ — The Rev. M. J. Berkeley, M.A., F.R.S.

Foliage of the Raspberry and Blackberry; *Lentinus scleroticola*, Murray; *Arenaria gothica*, Fries, in Britain; *Lilium Martagon*, naturalised in Worcestershire; *Carex laevigata*, Sm., var.; *Atriplex tatarica*, L.; Plants of North Bucks; *Euphorbia esula* in Northamptonshire.

„ 323. WILLIAMS: Revision of the Specific Forms of the Genus *Gypsophila*.

„ — WHITE, F. B.: A Puzzle in 'Topographical Botany' (Divisions of Perthshire).

„ — BENNETT, A.: Notes on some British Carices.

„ — SCULLY: *Juncus tenuis*, Willd. in Kerry.

„ — SPRUCE: *Lejeunea Rossettiana*, Massal. (a new Hepatic).

„ — SAUNDERS: Flora of the Ivel valley, Bedford.

„ — Welsh Records, 1889, *Erica vagans* near Bournemouth.

„ 324. PEARSON: A New British Hepatic (Plate 292).

„ — WHITWELL: *Arenaria gothica*, Fries, in Britain.

„ — The disappearance of British plants. (Second report of Committee.)

„ — DYER: John Ball, F.R.S.

Ulota calvescens, Wils. Mss., Carr. (*Vulota vittata*, Mitt.): Introduced Plants; *Rubus Hystrix*, in Salop; A Northamptonshire Potamogeton; *Plantago maritima*, L. form *pumila Kjellmanx* in the Faroe Is.

Journal of the Linnean Society, Botany. Vol. XXV.

No. 171. ROLFE: A morphological and systematic Review of the Apostasieæ. (Pl. XLVIII and 2 woodcuts.)

„ — MURRAY, G: On *Boodlea*, a new genus of Siphonocladaceæ.

„ — BARON: The Flora of Madagascar (with sketch-map).

„ — BAKER, J. G.: Further contributions to the flora of Madagascar. (Plates L–LIII.)

Journal of the Marine biological Association of the United Kingdom. New Series. Vol. I.

No. 2. POTTER: On the structure of the Thallus of *Delesseria sanguinea*. (Pl. XVII, XVIII.)

Journal and Transactions, The Pharmaceutical. Series 3.

No. 992. Alkaloids of the Potato Plant.
„ — Tanghinin.
„ — Gum from the Silver Wattle.
„ — RUSBY: Floral features of the Amazon valley (*concluded*).
„ 993. OGLE: The Composition of Tragacanth.
„ 995. DYMOCK AND WARDEN: *Picrasma Quassioides*, Benn.
„ 999. HOOPER: Musambra, a variety of East Indian aloes.
„ — HOLMES: Cultivation of Medicinal plants in Cambridgeshire.
„ 1000. HOOPER: *Balsamodendron Berryi*.
„ — Cinchona and Quinine production in India.
„ 1001. *Xanthoxylon Senegalense*.
„ — *Hippomane Mancinella*.
„ — Kola Nuts.
„ — *Polygala butyracea*.
„ — Cascara Sagrada.
„ — PAUL AND COWNLEY: Cinnamylcocaine in Coca leaves.
„ — Poisonous constituents of *Lactarius piperatus*.
„ 1004. MAIDEN: Botany Bay or *Eucalyptus Kino* (continued in 1009).
„ 1005. Mandragorine; Alkaloids in the poppy; Cubebs.
„ 1006. Notes on essential oils (continued in No. 1007).
„ 1007. SALMON: Senna pods.
„ 1012. DUNSTAN: The so-called Mussaenda Coffee of Reunion.
„ — MAIDEN: Sterculia Gum.
„ 1016. On *Scopolia Carniolica*.
„ — NAYLOR AND CHAPLIN: On the Root bark of *Euonymus* (Wahoo) and on Euonymin.
„ 1017. CRIPPS: The determination of the diastatic power of Extract of Malt.

Journal of the Quekett Microscopical Club. Ser. II, Vol. IV.

No. 25. RATTRAY: On some new species of Diatoms.

Journal of the Royal Agricultural Society of England. Series 2, Vol. XXV, Part 2.

COOKE, F. J.: On the value of Oil in Linseed Cake as a Food for Stock.

Journal of the Royal Microscopic Society. Transactions 1889.

Part 3. MASSEE: A Revision of the Trichiaceæ. (Plates V–VIII.)

Journal, Quarterly, of Microscopical Science. New Series, Nos. 118 and 119.

WALDEYER: Karyokinesis and its relation to the process of fertilisation (continued in No. 119).

Journal, Quarterly, of the Geological Society. 1889.

CANDLER: Observations on some undescribed Lacustrine Deposits at St. Cross, Sontis Elmham, Suffolk. (Plants, p. 507.)

Journal of the Royal Horticultural Society. Vol. XI, Part 2.

BAKER, J. G.: Notes on Saxifrages.
PAUL: The Cultivation of Saxifrages
REUTHE: Cultural and Descriptive Notes on Saxifrages.
BAARNART: Historical Notes on Dutch Hyacinths.

Journal of the Royal Horticultural Society (*continued*).

KERSTEN: The Cultivation of Hyacinths in Holland.

BURBIDGE: The Narcissus.

ENGLEHEART: Seedling Daffodils.

TAIT: Observations on Portuguese Narcissi.

VEITCH: Orchids: Past and Present.

Journal of the Society of Arts. Vol. XXXVII (*continued*).

No. 1916. Production of Persian Tombak (*Nicotiana Persica*).

„ —— Buhach (from *Pyrethrum cinerariæfolium*).

„ 1919. SIMMONDS: Olive Cultivation.

„ —— Coffee cultivation in Brazil.

„ —— Tobacco cultivation in Colombia.

„ 1920. Textile fibre of the Banana.

Lancet, The. 1889 (*continued*).

No. 3429. MACFARLANE: On the therapeutic action of Senna pods.

„ 3441. The typhoid germ.

„ 3446. The bacilli of Cholera, Typhoid, and Tuberculosis in Milk, Butter, and Cheese.

„ 3449. The 'Pellagra Bacillus.'

„ 3450. Bacteria and Virus.

„ 3456. MACLEOD: Dr. Klein's position with regard to the Comma Bacillus, and his replies to criticism answered.

„ 3458. HUEPPE AND WOOD: Investigations on the relation of putrefactive to parasitic bacteria.

„ 3461. STERNBERG: Recent researches relating to the Etiology of Yellow Fever.

Life-Lore. 1889. Vol. I (*continued*).

No. 7. GEDDES: Thorns and Prickles.

„ — HOUSTON: Natural history of Desmids (continued in Nos. 5–10).

„ 9. CHRISTY: Lords and Ladies.

„ 11. CROMBIE: Natural history of British lichens IV (continued in No. 12).

Vol. II.

No. 1. Natural defences of Plants.

„ 4. THOMAS, B.: The flagellate Algæ.

Magazine, Botanical, Curtis's. Series 3. Vol. XV (*continued*).

Nos. 535–540 contain plates and descriptions of:—*Pandanus labyrinthicus*, Kurz; *Syringa villosa*, Vahl.; *Olearia macrodonta*, Baker; *Disa lacera*, Sw., var. *multifida*, N. E. Brown; *Eucryphia pinnatifolia*, Gay; *Stapelia gigantea*, N. E. Brown; *Catasetum Garnettianum*, Rolfe; *Grevillea aspleniifolia*, Knight; *Berberis angulosa*, Wall.; *Anoiganthus brevifolius*, Baker; *Aristolochia hians*, Willd.; *Eucalyptus stricta*, Sieber; *Berberis Lycium*, Royle; *Eremurus himalaicus*, Baker; *Arachnanthe Clarkei*, Rolfe; *Draceena marmorata*, Baker, n. sp.; *Primula pusilla*, Wall.; *P. petiolaris*, Wall., var. *nana*, Hook. f.; *Fritillaria bucharica*, Regel; *Iris paradoxa*, Steven; *Shortia galacifolia*, Torr. and Gr.; *Carludovica rotundifolia*, Wendland MSS.; *Iris Bakeriana*, Foster; *Xylobium leontoglossum*, Benth.; *Phajus pauciflorus*, Blume; *Gerbera Jamesoni*, Bolus MSS.; *Thrinax excelsa*, Griseb.; *Tigridia Pringlei*, Wats.; *Cabomba aquatica*, Aub.; *Amorphophallus Eichleri*, Hook. f.; *Clintonia Andrewsiana*, Torrey.

Magazine, The Geological. New Series, Decade III, Vol. VI, No. 7.
GOODCHILD: On some modes of formation of Coal-seams.

Naturalist, The. (London and Leeds.) 1889 (*continued*).
No. 168. STRICKLAND: Notes on Fungi: with list of species collected in East Yorkshire (*concluded*).
„ 169. Algæ in Upper Swaledale—Twin flowering of *Chrysanthemum leucanthemum.*
„ 170. WOODD: Plants of Langstrothdale, Mid-west Yorkshire—*Polypogon monspeliensis*, near Horbury, South-west Yorkshire—Upper Teesdale Mosses.
„ 171. KIRK: Micro-Flora of Upper Teesdale, September, 1888.
„ — *Arenaria gothica*, Fries, a plant new to West Yorkshire.
„ 172. BAKER, J. G.: Plants of the Infer-Arctic Zone on Ingleboro' and Penyghent.
„ — ———————: On the varieties of *Arenaria ciliata.*
„ — ROTHERAY: The discovery of *Arenaria gothica* in W. Yorkshire.
„ — *Spiræa Filipendula* in Upper Airedale—Mosses at Robin Hood's Bay —*Cylindrospermum macrospermum* near Halifax.
„ 173. FOWLER: Lincolnshire Sand and Clay Plant.
„ — *Cephalozia Lammersiana* near Dewsbury.

Naturalist, The Essex. Vol. III.
Nos. 1-6.
POWELL: Epping forest Rubi.

Naturalist, The Midland. (London and Birmingham.) 1889 (*continued*).
No. 140. GROVE AND BAGNALL: The Fungi of Warwickshire (*continued*) (continued in No. 142).
„ — Botanical notes from South Beds.
„ 142. POULTON: Theories of Heredity.

Naturalist, The Scottish. (Perth.) 1889 (*continued*).
No. 25. BENNETT, A.: Additional records of Scottish Plants in 1889.
„ — BABINGTON: *Melampyrum Sylvaticum* in Caithness.
„ — PEYRITSCH: On the artificial production of Double Flowers, and of other abnormalities of structure (translated).
„ — WHITE, F. B.: The Collecting and Study of Willows.
„ — TRAIL: Revision of Scotch Discomycetes (continued in No. 26).
„ — Don's Plants—*Agrostris rubra*, L. in West Ross.
„ 26. WHITE, F. B.: *Poa palustris* in Perthshire.
„ — BENNETT, A.: A Nitella new to British flora (*N. batrachosperma*, A. Br.).

Nature. Vol. XL (*continued*).
No. 1034. WILLIAMS: The Sources of Nitrogen in Vegetation.
„ 1039. Report (Second) of the Committee appointed for the purpose of collecting information as to the disappearance of native plants from local habitats.
„ 1043. VINES: On Weissmann's Theory of Heredity.
„ 1045. On a new application of Photography to the demonstration of certain physiological processes in plants.
„ 1046. MIVART: Prof. Weismann's 'Essays.'
„ —— The Flora of China (Report of Committee).

Nature (*continued*).

No. 1048. ROMANES: Galls (origin of).
„ —— GARDINER: How plants maintain themselves in the struggle for existence.
„ 1049. CAMBOUÉ: Distribution of Animals, Plants, and Ocean Currents.
„ 1050. Galls (origin of) (see also No. 1052).

Papers and Proceedings of the Hampshire Field Club. No. 3.

EYRE: List of Hampshire Fungi, Part 2.

Proceedings of the Bristol Naturalists' Society. New series, Vol. VI.

Part 1. WHITE, J. W.: Flora of the Bristol Coal-field.
„ — BUCKNALL: The Fungi of the Bristol district.
„ — DALLINGER: On putrefactive organisms.
„ — JECKS: Suggestions as to the Causes of the difference in the colour between the Flowers and Foliage of Tropical and of temperate Regions.

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„ — COSTER: *Ajuga pyramidalis*, L., var. *reptans*, L.
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